To the Graduate Council:

I am submitting herewith a thesis written by Jonathan Paul Ambrose entitled "The Influence of Food Deprivation and Food Availability on Feeding Behavior in *Uca pugilator* (Bosc)." I have examined the final copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Ecology.

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THE INFLUENCE OF FOOD DEPRIVATION AND FOOD AVAILABILITY ON FEEDING BEHAVIOR IN *UCA PUGILATOR* (BOSC)

A Thesis

Presented for the

Master of Science

Degree

The University of Tennessee, Knoxville

Jonathan Paul Ambrose

August 1981

DEDICATED

to my mother and father

ACKNOWLEDGMENTS

I wish to thank my major professor, Dr. Harrison Ambrose, III, for his encouragement, criticisms, and financial support during the course of this project. I would also like to express my gratitude to my committee members, Dr. Arthur (Sandy) Echternacht and Dr. Gary McCracken, for their interest in my project, and for their patience and understanding during my periods of frantic last-minute paper shuffling.

Thanks are also in order for Mike Sloan and Mark Alston, fine graduate students both, and fellow "crabbers." Mike provided the map of the study area used in this thesis, and gave advice on soil analysis techniques. Mark provided me with a species list of aquatic vertebrates at the study site, and taught me how to throw a cast net.

To my wife, whose moral support and encouragement have helped me immensely throughout the course of this investigation, very special thanks are due.

Lodging and laboratory facilities at Rookery Bay National Estuarine Sanctuary were provided by the Collier County Conservancy, Collier County, Florida. I thank Dr. Kris Thoemke, Sanctuary Manager, and Dr. Bernard Yokel, Rookery Bay Marine Laboratory Director, for their invaluable aid in this regard.

Much of the cost of traveling to and from Rookery Bay Sanctuary was defrayed by travel funds from the Graduate Program in Ecology, and by a Grant-in-Aid of Research from Sigma Xi. A teaching assistantship from the Graduate Program in Ecology provided additional financial support during the course of this project.

ABSTRACT

The sand fiddler crab, *Uca pugilator* (Bosc), is a semiterrestrial burrowing crab which lives in intertidal areas along the Eastern and Gulf coasts of the United States. Like other fiddler crabs, *U. pugilator* feeds by sorting soil particles with its mouthparts. Unlike most other fiddler crab species, however, *U. pugilator* lives in an exposed, barren habitat characterized by sandy soils; these soils provide a relatively impoverished food source for this species.

The basic intent of this study was to determine the effect of food deprivation and food availability on various subcomponents of the overall feeding behavior of *U. pugilator*. These subcomponents, which served as categories for data collection, included: (1) feeding rates, measured as the total number of feeding motions made by a crab's feeding claw(s) per minute; (2) lengths of feeding periods, estimated by the ratio of feeding to nonfeeding crabs throughout a daily activity period; and (3) distances traveled during feeding periods, measured as the absolute or relative distance from a feeding crab to its burrow. Data were collected for each of these behavioral categories by direct observation of individual sand fiddler crabs subjected to varying periods of food deprivation; observations were likewise made on individual crabs in areas whose substrates had been enriched, to various degrees, by the addition of food.

Food resource distribution in the habitat of *U. pugilator* was determined by quantitative organic carbon analysis of soil samples.

Field extraction efficiencies for this species were estimated by comparing the organic carbon levels of foraged and unforaged substrate. Laboratory experiments of the sand fiddler's feeding behavior investigated the crab's ability to detect food levels in the substrate, and examined the influence of sexual dimorphism on feeding behavior.

Results of this study indicate that both food deprivation and substrate food availability may affect the length of feeding periods, as well as distances traveled during feeding periods. The length of time that crabs feed, and their location during the feeding process, may in turn greatly influence the crabs' risks of predation, dessication, and hyperthermia. Neither food deprivation nor substrate food availability appears to affect feeding rates, however. Males fed at approximately 2/3 the rate of females in all experiments in this study, indicating that intersexual differences in feeding rates are probably a result of sexual dimorphism in this species.

Uca pugilator can apparently detect small differences in the food levels of adjacent substrates, and can change its feeding behavior in response to perceived food levels. The feeding activities of this species result in a significant short-term decrease in the organic carbon levels of the foraged substrate, but the long-term effect of its feeding and burrowing activities may be an increase in food availability in some areas. Thus, *U. pugilator* modifies its feeding behavior according to gradients of food density in its habitat, and through its foraging and burrowing activities may actually create new gradients in food density.

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I. INTRODUCTION

Uca pugilator, the sand fiddler crab, is a brachyuran decapod native to the Eastern and Gulf coasts of the United States. Its geographic range extends from the northern shore of Cape Cod, Massachusetts, southward as far as the Bahamas, and westward as far as Corpus Christi, Texas (Crane, 1975). *Uca pugilator* is one of the relatively few species of fiddler crabs whose range reaches into the temperate zone, and which shows specific behavioral and physiological adaptations for survival in seasonally-variable temperature regimes (Vernberg, 1959; Vernberg and Tashian, 1959; Miller and Vernberg, 1968; Smith and Miller, 1973).

The sand fiddler crab is found primarily on intertidal mud flats, or on sandy shores which are protected from direct wave action. This crab's physiological dependence upon periodic submersion prevents it from inhabiting areas far landward from the intertidal zone, and its behavioral avoidance of deep water restricts movements out into the littoral zone. Thus, like other fiddler crabs, this species remains physiologically aquatic, but is behaviorally terrestrial (Herrnkind, 1968a; Bliss, 1968). Sand fiddlers make their homes in burrows that extend downward to water-saturated soil, but virtually all activity is restricted to the surface of the substrate.

The daily activity pattern of *U. pugilator* is largely regulated by the tides. During the ebb tide, the crabs emerge from their burrows and move downslope with the receding water. On the rising tide, the

crabs move upslope and reenter the burrows, sometimes plugging the entrances with sand before flood tide arrives. All activities, including feeding, courtship, copulation, and agonistic encounters, are thus influenced by the tidal cycle.

In most *Uca* species, individual crabs confine their activities to an area of substrate surrounding a specific burrow site. In *Uca pugilator* populations, an additional behavior known as "hording" or "droving" frequently occurs, in which members of the population aggregate in great numbers along the intertidal slope to feed during low tide. These large aggregations may contain several thousand crabs of both sexes. Territorial behavior seems to be suppressed in hording crabs, as individuals in the dense groups show an unusual degree of tolerance toward each other. Hordes are usually derived from populations of crabs living in the higher areas of sloping intertidal beaches; rarely are these feeding associations found in sand flat areas (Herrnkind, 1968a). Hording behavior is common only in the southern part of the sand fiddler's range. The environmental or physiological inducements for this unusual form of social behavior are unknown.

Early accounts of the biology of *U. pugilator* were primarily observational in nature, and dealt with the more conspicuous aspects of the ecology and behavior of this species. Bosc (1802, cited in Crane, 1975) provided the first written description of the crab's habitat, habits, and color. Say (1817-1818, cited in Crane, 1975), Kingsley (1888), Pearse (1914), Hyman (1920, 1922), and Dembowski (1926, cited in Crane, 1975) provided information about the sand fiddler's behavior and habitat in various locations throughout its range.

More recently, *U. pugilator* has become a popular subject for experimental studies of decapod behavior. Aspects of the sand fiddler's behavioral repertoire which have received recent attention from researchers include: visual communication (Crane, 1943, 1957, 1975; Salmon, 1965, 1967; Salmon and Atsaides, 1968; Salmon et al., 1978; Schöne, 1968; Hyatt, 1977a,b); acoustical communication (Crane, 1943; Burkenroad, 1947; Salmon, 1965, 1967, 1971; Salmon and Stout, 1962; Salmon and Atsaides, 1968, 1969; Salmon and Horch, 1972; Salmon and Hyatt, 1979; Horch and Salmon, 1969; Horch et al., 1980; Hyatt, 1977a); agonistic behavior (Schöne, 1968; Hyatt, 1977a; Hyatt and Salmon, 1978, 1979); visual orientation (Herrnkind, 1966, 1967, 1968a, 1972; Young and Ambrose, 1978); and tidal and circadian rhythmicity of activity (Fingerman, 1957; Barnwell, 1966, 1968).

Feeding behavior in *Uca pugilator* has been described by several authors, including Crane (1975), Miller (1961), and Robertson et al. (1980). In contrast to the predaceous habits of their zoeal stages (Herrnkind, 1968b), adult sand fiddlers are deposit feeders, gaining nourishment from organic materials in the upper 3 to 5 mm of sandy soils (Kraeuter, 1976). In the process of feeding, small portions of substrate are carried to the buccal cavity by the minor chelae, or feeding claws. Inside the buccal cavity, water from the gill chambers is bubbled and circulated rapidly to facilitate the separation of coarse sand grains from silt particles and detritus via differential flotation rates (Miller, 1961).

After the substrate particles have been sorted, the mouthparts pass the finer materials upward into the mouth; coarse sand particles

are ejected by the mouthparts and form small, moist pellets at the buccal cavity opening. These feeding pellets are transferred to the ground by the minor chelae, or alternatively, are simply allowed to fall from the buccal cavity opening (Crane, 1975).

During the flotation sorting process, large soil particles are subjected to the scouring action of hundreds of spoon-shaped bristles located on the second maxillipeds. This scouring action removes organic materials clinging to the sand grains (Miller, 1961).

In male fiddler crabs, the major chela is used primarily in courtship displays, sound production, and combat; it is unsuitable for assisting in the feeding process, except as a means of defending a feeding area. Therefore, male fiddler crabs have only one feeding claw, while females have two. Kingsley (1888) and Hyman (1920) noted that sexual dimorphism in fiddler crabs results in females feeding at a faster rate than males. Valiela et al. (1974) demonstrated that in *Uca pugnax*, males compensate for their slower feeding rate by feeding for longer periods than females.

The diet of *Uca pugilator* has been investigated to ascertain which organic substrate components are actually ingested and metabolized. Pitts and Cowley (1974) indicated a red yeast, *Rhodotorula mucilaginosa*, as a major dietary component of *U. pugilator*, on the basis of its abundance in the crab's midgut. Subsequent feeding experiments (Chrzanowski and Cowley, 1977; Cowley and Frye, 1978) have demonstrated that, although diets of pure yeast are unsuitable for sand fiddler nutrition, yeasts may play an important role in the diet by supplying necessary B-vitamins.

Haines and Montague (1979) compared carbon 13:carbon 12 ratios of the fecal pellets of *U. pugilator* with the C13:C12 ratios of various plant materials in its habitat, and concluded that vascular plant-derived detritus is the sand fiddler's main source of nutrition. Smith and Miller (1973) and Robertson et al. (1980) have shown that fiddler crabs ingest large quantities of diatoms. Teal (1958) found that *U. pugilator* can survive with no apparent ill effects on a diet of pure bacteria.

Other items in the sand fiddler's diet may include algae, protozoans, and nematodes (Crane, 1975; Robertson et al., 1980). The discovery of a collagenolytic protease in the hepatopancreas of *U. pugilator* (Eisen and Jeffrey, 1969; Eisen et al., 1973; Grant et al., 1980) indicates that animal-derived detritus may also be an important dietary component. *Uca pugilator* has been observed feeding on dead fish (H. W. Ambrose, personal communication) and mammalian feces (Crane, 1975).

Extraction efficiencies and assimilation efficiencies for *Uca* have received little attention from researchers, possibly because of uncertainties as to the choice of relevant measurable parameters for species with rather catholic dietary habits. Valiela et al. (1974) compared levels of organic carbon in fecal pellets of *U. pugnax* to those in substrate samples, but gave no information as to which materials were assimilated during digestion. Robertson et al. (1980) compared levels of chlorophyll a and adenosine triphosphate (ATP) in the substrate and feeding pellets of *U. pugilator,* in order to estimate

extraction efficiencies. Their estimates were based on living biomass indicators, however, and therefore did not measure the crabs' extraction efficiencies for detritus.

Estimates of food availability and distribution in the habitats of *U. pugilator* have likewise been rare. Robertson et al. (1980) found large differences in the chlorophyll a and ATP levels of two different sand fiddler habitats on Sapelo Island, Georgia. They did not, however, provide detailed information on the spatial distribution of food within each of the habitats.

In the intertidal zones of southwestern Florida, the substrate of sites occupied solely by *U. pugilator* is apparently much lower in organic matter than that in the mud flats and mangrove shores inhabited by other *Uca* species. Average organic carbon content in *U. pugilator* site substrates is approximately 1/10 of that at *U. rapax* sites, and 1/50 of that at *U. thayeri* sites (Sloan, personal communication). Thus, the sand in *U. pugilator* sites probably represents a relatively impoverished food source, as compared to substrates at the sites of *U. rapax* or *U. thayeri*.

The amount of time that a sand fiddler crab spends feeding on the surface of the substrate may have great ecological significance in terms of its ability to avoid predation and to maintain thermal and osmotic homeostasis. Because of its coloration and size, *U. pugilator* is a conspicuous organism when it is active on the intertidal slopes; almost all predation on the crab occurs during this segment of its activity cycle (Crane, 1975; Aspey, 1978). In addition, a fiddler crab on the

sand surface constantly faces the problems of hyperthermia and dessication, while conditions in its burrow are thermally and osmotically more stable (Teal, 1958; Vernberg and Tashian, 1959; Wilkens, 1960; Bliss, 1968; Powers and Cole, 1976).

Weather and the tidal cycle place limitations on the amount of time that sand fiddler crabs can remain active each day. In addition to forced inactivity during high tide, cold or stormy weather can greatly restrict the activities of fiddler crabs, resulting in different levels of food intake from day to day. Thus, it is conceivable that differences in the food satiation levels of crabs might find expression in differences in the amount of time the crabs spend feeding, or in the distances they will travel during a given foraging period, or in their feeding rates.

Little or no research has been directed toward this aspect of the foraging behavior of fiddler crabs. It is this area which this study encompasses, in an effort to address the following questions:

1. Does the relative hunger state of *U. pugilator* individuals determine or influence their daily movements, their rates of feeding, or the lengths of their foraging periods?

2. Does substrate food availability serve as an environmental cue which can determine or influence foraging behavior in sand fiddler crabs?

In order to provide answers to the above questions, it was necessary to include in the study the following specific areas of investigation:

1. Observation of "normal" patterns of daily foraging behavior in *U. pugilator,* including movements of individual crabs, feeding rates, and lengths of foraging periods.

2. Examination of the foraging behavior (as described by the parameters mentioned above) of crabs at different levels of artificially-induced food deprivation, produced by subjecting groups of confined crabs to different feeding schedules.

3. Investigation of foraging behavior in crabs exposed to different levels of food availability, produced by differential enrichment of the substrate.

4. Determination of the heterogeneity or homogeneity of food resource distribution in the natual habitat substrate, by quantitative soil analysis.

5. Estimation of the extraction efficiencies of *Uca pugilator* on natural and artificially-enriched substrates.

II. DESCRIPTION OF THE STUDY AREA

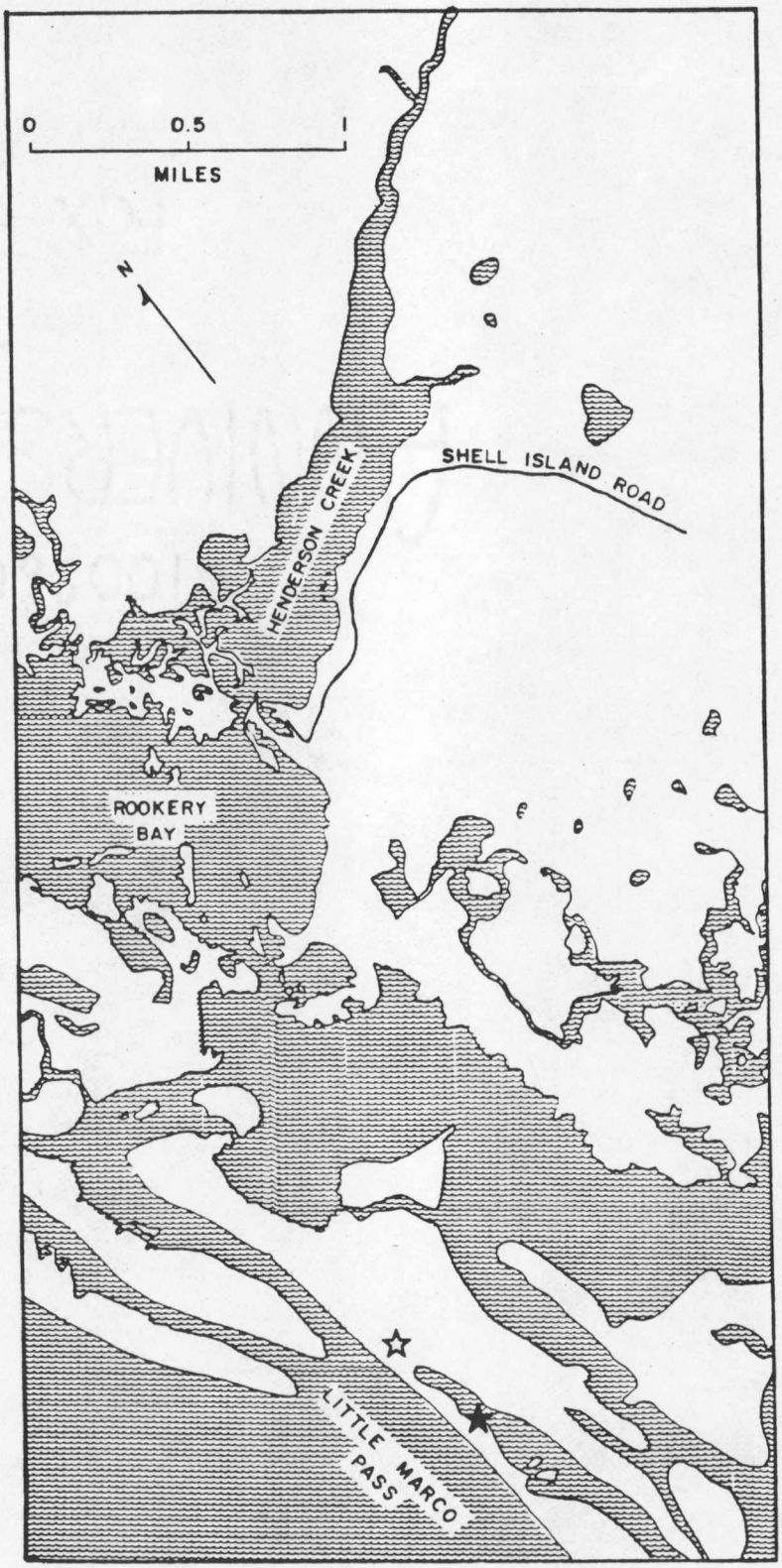
Rookery Bay National Estuarine Sanctuary is located approximately 8 km south of Naples, Florida, on the southwestern coast of the state. Within the sanctuary boundaries exists a variety of natural and disturbed habitats that range from terrestrial to riparian. The total area of the sanctuary is 1,620 hectares, much of which is regularly or periodically inundated by Henderson Creek, the estuary's main freshwater source. Mean annual rainfall at this location is 119 cm, with the majority of the precipitation occurring from April to September. Mean monthly temperatures for June and December are 29°C and 19°C, respectively.

At the mouth of Rookery Bay Estuary lie several small barrier islands; one of these small sandy islands is located in the area known as Hurricane Pass (Figure 1). As its name suggests, Hurricane Pass was formerly a shallow waterway between two islands. Siltation along the northwestern end of this waterway has recently united the two land masses into a single, larger island. Thus, the island today has an elongate central bay which is daily filled and drained through an inlet on its southeastern border. On both sides of this central bay are protected sandy beaches with an intertidal zone 8 to 10 meters wide.

Above the bare intertidal beaches, the vegetation consists mainly of cordgrass (*Spartina alterniflora*), sea purslane (*Sesuvium* sp.), and red mangrove seedlings (*Rhizophora mangle*). Farther from the beach zone, the vegetation includes cabbage palmetto (*Sabal palmetto*), saw-palmetto

Figure 1. Map of the study area, showing Henderson Creek, Rookery Bay, and the Hurricane Pass area.

The study site is due east of Little Marco Pass. An open-centered star shows the approximate location of the supratidal sand flat. A solid star marks the location of the intertidal beach. (Map courtesy of Michael C. Sloan).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BAY
LITTLE MARCO
PASS

Figure 1.

(*Serenoa repens*), coconut palms (*Cocos nucifera*), Australian pines (*Casuarina equisetifolia*), red mangroves (*Rhizophora mangle*), white mangroves (*Laguncularia racemosa*), black mangroves (*Avicennia nitida*), and fig trees (*Ficus* spp.).

At the northwestern end of the bay, the accumulation of sand and silt has created a supratidal sand flat. Vegetation in this area is very sparse, and consists mainly of sea purslane, seablite (*Suaeda linearis*), scattered red mangrove seedlings, and an unidentified grass.

During the period of field investigation, November 30-December 20, 1980, the sand fiddler crabs in the study area comprised two behaviorally segregated populations. The first group consisted of "hording crabs" living on the intertidal slopes of the central bay. These sand fiddlers built their burrows in the supratidal *Spartina* area, and foraged on the intertidal slopes in large, dense aggregations of several hundred to approximately three thousand crabs. The other behavioral population consisted of a group of crabs living in the supratidal sand flat area. Sand fiddlers in this group restricted their ambulations to areas surrounding their burrows, and did not form gregarious feeding associations. These crabs will be referred to as "burrow crabs."

Members of the terrestrial animal community observed at the study site during the period of investigation included raccoons (*Procyon lotor*), nine-banded armadillos (*Dasypus novemcinctus*), cotton rats (*Sigmodon hispidus*), Louisiana herons (*Hydranassa tricolor*), white ibises (*Eudocimus albus*), brown pelicans (*Pelacanus occidentalis*), semipalmated plovers (*Charadrius semipalmatus*), Wilson's plovers

(*Charadrius wilsonia*), and green anoles (*Anolis carolinensis*). Shorebirds seen at the study site at other times of the year include common egrets (*Casmerodius albus*), reddish egrets (*Dichromanassa rufescens*), willets (*Catoptrophorus semipalmatus*), green herons (*Butorides virescens*), and laughing gulls (*Larus atricilla*).

Fishes of the central bay included Gulf menhaden (*Brevoortia patronus*), Atlantic needlefish (*Strongylura marina*), sheepshead minnows (*Cyprinodon variegatus*), long-nose killifish (*Fundulus similis*), pinfish (*Lagodon rhomboides*), striped mullet (*Mugil cephalus*), mojarras (*Eucinostomus* sp.), and Atlantic stingrays (*Dasyatis sabina*). Aquatic molluscs observed at the study site were: *Macrocallista nimbosa*, *Polinices duplicata*, *Cerithidea scalariformis*, *Busycon perversum*, *Melongena corona*, *Littorina angulifera*, *Telebra* spp., *Fasciolaria tulipa*, and *Fasciolaria distans*. Aquatic arthropods of the central bay included horseshoe crabs (*Limulus polyphemus*), hermit crabs (*Pagurus* spp.), and blue crabs (*Callinectes sapidus*).

III. MATERIALS AND METHODS

Field Experiments

Field experiments of the sand fiddler's feeding behavior were conducted within the supratidal sand flat area and along the central bay's intertidal beach zone. A pair of 7X binoculars was used to observe individual crabs in each area. Observational data were recorded in field notebooks, and on a portable tape recorder.

During field experiments requiring the displacement of individual crabs from the study site, crabs were housed temporarily at the Shell Point Laboratory Facility in Rookery Bay Sanctuary. This laboratory facility is located approximately 4.2 km from the study site. The crabs were kept in 12-liter plastic buckets which were filled to a depth of 1 cm with seawater from the study area. Throughout their period of confinement at the facility, the crabs were exposed to ambient air temperatures, but were protected from direct sunlight.

Crabs which were fed during the confinement period were given Tetramin brand fish food. Tetramin is a food which is readily accepted by *U. pugilator*, and which has served as the primary source of nutrition for several laboratory-maintained populations of sand fiddlers at The University of Tennessee.

Noon air temperatures at the study site ranged from 23°C to 27°C during the period of investigation. Noon water temperatures, taken at a depth of 30 cm in the central bay, varied from 22°C to 24°C. Carapace

widths of crabs used in the field experiments ranged from 1.7 cm to 2.5 cm. All crabs used in the experiments were adults.

A. Normal feeding patterns in burrow crabs and hording crabs

In order to assess the effects of food deprivation and food availability on the feeding behavior of *U. pugilator*, it was necessary to first observe and characterize the normal feeding patterns of burrow crabs and hording crabs. In both of these behavioral groups (referred to as "control burrow crabs" and "control hording crabs," respectively), feeding rates of individual crabs were calculated as the number of substrate-to-mouth movements of the minor chelae that the crabs performed per minute. Crabs were judged to be in a feeding mode of behavior if they performed at least one substrate-to-mouth movement every five seconds. A preliminary investigation of feeding rates had indicated that this method of designating feeding and nonfeeding crabs was preferable to simple random selection and observation of crabs, since it eliminated the problem of calculating feeding rates for crabs which were not primarily feeding. Previous experience had shown that if a crab failed to perform one feeding motion in a given five-second period, probabilities were high that the observed crab was involved in a completely different or conflicting behavioral routine (e.g., burrow maintenance, combat, or courtship). Observations of feeding and nonfeeding crabs were made from a distance of three to five meters, using 7X binoculars and an electronic digital stopwatch.

Distances traveled during foraging periods were calculated differently for burrow crabs and hording crabs. In the burrow crab area, the foraging distance of an individual crab was measured as the distance that the crab moved from its burrow in three minutes' foraging time. In order to calculate this distance, a feeding crab was first scared into its burrow; when the crab reemerged from its burrow and resumed feeding, it was observed for three minutes. At the end of this period, its distance from the burrow was determined by placing a pencil in the sand at the spot the crab's central carapace had been, and measuring from this marker to the burrow entrance with a meter stick. Crabs were observed from a distance of two to three meters.

In the intertidal beach zone, hording crabs foraged 10 meters or more from their burrows, which were hidden in the tall *Spartina* grass. The high density of the feeding crabs, and their apparent lack of territoriality, made it impossible to visually associate an individual crab with its burrow. Foraging distances in the hording crab area were therefore calculated on the basis of an individual crab's relative position on the intertidal slope at low tide. A 30-meter measuring tape and wooden dowel markers were used to divide a 1-meter wide section of the intertidal slope into upper, middle, and lower beach segments, each of which corresponded to 1/3 the length of exposed beach. Approximately 15 minutes after this demarcation of the beach, hording crabs in each zone were observed from the supratidal *Spartina* grass area. Estimates of the number of crabs in each section of beach were obtained with the aid of binoculars and a hand-held tally counter.

B. Burrow-covering experiment

Within the burrow crab area, the effects of food deprivation produced by long periods of confinement in burrows on the sand fiddler's feeding behavior were investigated. Approximately three hours before maximum low tide, two large plywood sheets, each measuring 0.8 m X 1.5 m, were placed flat on the ground to cover the burrow entrances of from 14 to 20 fiddler crabs. These plywood sheets were left in place for 48 hours; after this period, the sheets were removed, uncovering the burrows. During the confinement period, the crabs whose burrow entrances were covered did not dig themselves out from underneath the plywood sheets.

Observation of the previously burrow-confined crabs began 30 minutes after removal of the plywood sheets. A preliminary experiment had shown that this time period was sufficiently long to allow the crabs to resume normal feeding behavior, but was not long enough to allow feeding crabs to become satiated and stop feeding. Feeding rates, foraging distances, and numbers of feeders and nonfeeders were obtained in the same manner as for the "normal" or "control" burrow crab population. This experiment was repeated four times, and the locations of the two plywood sheets were shifted at each repetition.

C. Burrow crab enclosure experiment

In order to determine the effects of food deprivation and substrate food availability on the feeding behavior of burrow crabs, members of the population were removed from the study site, subjected to one of

two different feeding schedules (food given ad libitum vs. no food) for a 48-hour period, and then released onto normal or artificially-enriched substrates within one of four circular enclosures built on the sand flat. The enclosures were made by inserting 25 cm wide strips of aluminum flashing material 10 cm into the soil to form circular arenas 1 m in diameter with 15 cm high walls. The four enclosures were placed close together in a 2 X 2 pattern within the burrow crab area, in a region that had no burrows.

Crabs used in this experiment were dug from their burrows with a shovel, placed into plastic buckets, and transported to Shell Point Laboratory Facility. Here they were randomly sorted into two groups of 20 crabs (10 males and 10 females) each. One group was deprived of food for 48 hours; the other group was given Tetramin fish food ad libitum for the same period of time.

After 48 hours, the crabs were returned to the study site. Before the crabs were released into the arenas, the substrates of two of the enclosures were enriched by adding an extract of animal and plant tissues. This extract was prepared by combining approximately 0.5 l of algae-covered aquatic grass from the island's central bay with 4 l seawater and 2 g Tetramin flakes. The mixture was stirred for approximately three minutes, and was then strained through cotton cloth to remove large food particles. Two liters of the food solution were applied to the substrates of each of two of the enclosures. Each of the other two enclosures received an application of 2 l seawater.

The crabs were released into the enclosures 1.5 hours after maximum low tide. Half of the starved crabs (five males and five females) were placed in an enriched substrate enclosure, and half were placed in an unenriched substrate enclosure. The fed crabs were distributed in the remaining two enclosures in the same manner.

Observation of the feeding behavior of these crabs began 30 minutes after their release into the enclosures. Feeding rates and numbers of feeders and nonfeeders were obtained as in the control burrow crab population. At one hour after release, the number of crabs on the sand surface and the number of crabs which had dug and entered burrows were recorded for each of the enclosures. The crabs were then removed from the arenas. This experiment was repeated twice.

D. Hording crab enclosure experiment

An enclosure experiment was conducted in the intertidal beach zone in order to compare the feeding behavior of starved and fed hording crabs on enriched and unenriched substrates. Strips of aluminum flashing material 25 cm wide were used to construct four adjacent rectangular enclosures oriented perpendicularly to the shoreline; these enclosures were 1 m wide and 8.5 m long, open-ended downslope and closed at the upslope end. Each enclosure extended from just below the supratidal vegetation line to the water's edge at low tide, and was almost completely inundated at high tide.

Hording crabs were collected from the intertidal slope and transported to Shell Point Laboratory Facility. Feeding and starvation

methods were identical to those employed in the burrow crab enclosure experiment. The larger area of the hording crab enclosures necessitated the addition of 16 l of food extract per enclosure to achieve an enrichment level roughly equal to that in the burrow crab enclosure experiment. The unenriched hording crab enclosures each received 16 l seawater.

Hording crabs were released into the enclosures one hour after maximum low tide. Thirty starved crabs (15 males and 15 females) were placed in one of the enriched substrate enclosures, and another 30 starved crabs were similarly released in an unenriched substrate enclosure. Fed crabs were distributed in the other two enclosures in the same manner.

Thirty minutes after release, feeding rates and numbers of feeders and nonfeeders were obtained for each of the four behavioral groups. In addition, the number of crabs within 60 cm of the water's edge was recorded for each of the enclosures at this time. At one hour after release, the numbers of crabs on the sand surface and crabs in burrows were recorded for each of the enclosures. The crabs were then removed from the enclosures. This experiment was repeated three times.

Substrate Food Distribution and Field Extraction Efficiencies

In December 1980, six 15-meter line sampling transects were established within the study area. Five of these transects were located in the supratidal sand flat area. The remaining transect

was located on the intertidal beach slope, parallel to the shoreline, and 4 m from the supratidal vegetation line. Samples of the upper 5 mm of unforaged substrate were obtained at three-meter intervals along each of these transects. Feeding pellets were collected from areas immediately adjacent to each of the substrate sampling points.

Two additional 15-meter line sampling transects were established on the intertidal beach slope in May 1981. These transects were also parallel to the shoreline, and were 1 m and 7 m, respectively, from the supratidal vegetation line. Substrate and feeding pellet samples were obtained along these two transects as in the previous transects.

The substrate and feeding pellet samples from all transects were air dried. The samples were then chemically analyzed for quantitative determination of organic carbon, using the Walkley-Black method (Allison, 1965). This method of soil analysis was chosen because of its simplicity of procedure and its accuracy of estimation for a wide range of soil types, including sandy soils.

Levels of organic carbon in the substrate samples were compared to determine the homogeneity or heterogeneity of food distribution in the study area. Levels of organic carbon in feeding pellet samples were compared to those in substrate samples to determine extraction efficiencies of *Uca pugilator* within the study site.

Laboratory Experiments

From February 1981 to April 1981, laboratory experiments of feeding behavior in *U. pugilator* were conducted at The University of Tennessee

campus in Knoxville, using hording crabs which had been removed from the field study area in December 1980. The laboratory crab population was maintained in three 60 X 121 X 47 cm plastic tubs filled with sand. A recirculating-fluid pumping system subjected the crabs to semidiurnal tides. Artificial seawater for the crabs was prepared from a standard dilution of Instant Ocean brand commercial marine mix (specific gravity = 1.023 at 20°C).

Air temperature in the laboratory during the period of experimentation was 24°-26°C. Water temperature in the plastic tubs remained at 23°-24°C. Carapace widths of the crabs used in the laboratory experiments ranged from 1.9 cm to 2.5 cm. All crabs used in the experiments were adults.

A. Feeding choice experiment

The following experiment was conducted to investigate the ability of *U. pugilator* to detect differences in the food levels of two adjacent substrates. A 38-liter aquarium with a 25 X 50 cm floor was divided into two 25 X 25 cm halves, using a 1.3 cm high plastic strip as a partition. In one half of the tank was placed 1,160 g washed and dried sand, which had been moistened with 200 ml artificial seawater. This substrate was compacted and leveled to a depth of 1.3 cm. The substrate placed in the other half of the tank was identical to the first mixture except for the addition of 5.8 g finely-ground Tetramin flakes. This addition represented a 0.5% food enrichment by weight. The feeding choice trials were repeated at 0.1%, 0.05%, and 0.01% substrate enrichment levels.

Six crabs (three males and three females) were removed from the laboratory-maintained population, and were placed singly into 500 ml cylindrical plastic containers. Fifteen ml artificial seawater was added to each container. After 24 hours, the crabs were removed from the containers, rinsed in artificial seawater, released into the middle of the experimental tank, and allowed to forage for one hour.

After one hour, the crabs were removed from the tank. Feeding pellets found in each half of the tank were collected, dried, and weighed to determine any differences in the amount of substrate processed in each half. Levels of organic carbon in the feeding pellets were determined by the Walkley-Black method, and were compared to the organic carbon levels of unforaged substrate to determine food extraction efficiencies by the crabs. At each level of substrate enrichment, three replicate tanks, each containing six crabs, were used. The entire experimental procedure was then repeated, at all four enrichment levels, using crabs which had been fed Tetramin flakes ad libitum during the 24-hour confinement period.

B. Feeding claw amputation experiment

Earlier experiments in this study had indicated that intersexual differences in the sand fiddler's feeding behavior might be due to sexual dimorphism (i.e., males have only one feeding claw while females have two). Sexual dimorphism apparently greatly influences feeding rates, and feeding rates may determine the lengths of foraging periods (and therefore the amount of time that sand fiddlers are exposed to the

risks of predation, dessication, and hyperthermia). The following experiment was therefore conducted to ascertain the effects of the loss of a feeding claw on the feeding behavior of female sand fiddler crabs.

Thirty female crabs were selected from the laboratory-maintained population. The left minor chela of 10 of the crabs was removed by severing the limb between the basis and ischium (the site of autotomization of limbs in fiddler crabs). In the second group of 10 crabs, the left first ambulatory leg was removed between the basis and ischium. This group served as a control for behavioral changes resulting from the amputation process itself. Crabs in the third group had no limbs removed.

Eight grams of finely-ground Tetramin flakes were added to 12 liters moist sand and mixed thoroughly. This mixture was then divided equally between six 15 X 26 cm plastic containers. The sand in each container was compacted and leveled to a depth of 4 cm.

The crabs were starved for 48 hours, then released in groups of five into the six plastic containers. Feeding rates and numbers of feeders and nonfeeders were recorded for each group at one-half, one, two, and three hours after release. At three hours after release, the numbers of crabs on the sand surface and crabs in burrows were recorded for each of the three behavioral groups. The crabs were then removed from the containers. This experiment was repeated three times.

Statistical Analysis of Data

Distributions of feeding rates for each experimental group were tested for normality. Assumptions of homogeneity of variance were met, as indicated by the F-max test (Sokal and Rohlf, 1969). Analysis of variance (ANOVA) was used to test for statistically-significant differences in the feeding rates of different experimental groups. Distributions of foraging distances in the burrow crab groups were also tested for normality and homogeneity of variance. Analysis of variance was used to test for significant differences in the foraging distances of the control and burrow-confined crab groups. This statistical method was also used to test for significant differences in the organic carbon levels of substrate and feeding pellet samples. Analysis of variance was chosen for these comparisons because of its applicability in testing differences between the group means of continuous data, and because of its relative robustness with respect to nonnormal distributions (in some cases, normality of data was difficult to determine because of small sample sizes).

The chi-square test of independence of samples (Sokal and Rohlf, 1969) was used to test for significant differences in the relative positions of hording crabs on the intertidal beach slope. This same method was used to test for significant differences in the feeder:non-feeder ratios of different behavioral groups, and to test for significant differences in the ratios of surface-active crabs to crabs in burrows among the enclosure experiment groups. The chi-square test was

employed for these comparisons because of its usefulness in determining inequalities between the frequency distributions of discrete, nominal data.

The 0.05 probability level was chosen as the level of significance for all statistical tests in this study. All error terms that were calculated were expressed as standard deviations from means.

IV. RESULTS

Field Experiments

A. Normal feeding patterns in burrow crabs and hording crabs

Analysis of variance of the feeding rates (measured as the total number of feeding claw movements per minute) of control burrow crabs and control hording crabs showed that, in both groups, feeding rates differed significantly between the sexes. However, no significant difference was found between the feeding rates of male burrow crabs and male hording crabs, nor between the feeding rates of female burrow crabs and female hording crabs (Table 1). The mean feeding rate of male burrow crabs was 42.9 ± 6.9 movements/minute (all error terms are expressed as standard deviations from the mean), and the mean feeding rate for male hording crabs was 41.3 ± 9.1 movts./min. Average feeding rates for female burrow crabs and female hording crabs, respectively, were 67.0 ± 11.8 movts./min. and 70.5 ± 9.4 movts./min.

Contingency table analysis of feeder:nonfeeder ratios for males (feeders:nonfeeders = 239:23) and females (feeders:nonfeeders = 85:24) in the control burrow crab group indicated that a significantly larger portion of the male subgroup could be classified in the "feeder" category ($\chi^2 = 12.19$; $p < 0.05$; Table 2). In the burrow crab area, considerably more males were active on the surface of the sand than were females (262 males vs. 109 females). Actual sex ratios in the study area were impossible to determine without digging up the crabs

TABLE 1

ANALYSIS OF VARIANCE SUMMARIES FOR FEEDING RATES OF BURROW CRAB AND HORDING CRAB CONTROL GROUPS

Source	D.F.	S.S.	M.S.	F
Comparison of feeding rates of male burrow crabs and male hording crabs.				
Between groups	1	23.45	23.45	0.41
Within groups	41	2372.59	57.87	
Total	42	2396.04		
Comparison of feeding rates of female burrow crabs and female hording crabs.				
Between groups	1	98.03	98.03	0.78
Within groups	38	4769.17	125.50	
Total	39	4867.20		
Comparison of feeding rates of male and female burrow crabs.				
Between groups	1	8530.79	8530.79	92.36*
Within groups	57	5264.70	92.36	
Total	58	13795.49		
Comparison of feeding rates of male and female hording crabs.				
Between groups	1	5068.63	5068.63	59.41*
Within groups	22	1877.06	85.32	
Total	23	6945.69		

*Significant at the 0.05 level.

TABLE 2

NUMBERS OF FEEDERS AND NONFEEDERS —
CONTROL BURROW CRAB GROUP

	Feeders	Nonfeeders
Males	239 (228.81)	23 (33.19)
Females	85 (95.19)	24 (13.81)

Values in parentheses are expected frequencies.

$\chi^2 = 12.19$; d.f. = 1; $p < 0.05$.

in burrows; since this would result in extensive disturbance to the study area, it was not attempted.

Contingency table analysis of the feeder:nonfeeder ratios for control hording crab males (154:39) and control hording crab females (121:43) revealed no significant difference between the two groups ($\chi^2 = 1.80$; $p > 0.05$; Table 3). The difference between the numbers of observed males (193) and females (164) in the hording crab area was smaller than that in the burrow crab area, although males were still the predominant sex.

Contingency table analysis of feeder:nonfeeder ratios for control burrow crab males (239:23) and control hording crab males (154:39) indicated a significantly higher percentage of feeders among burrow crab males ($\chi^2 = 12.33$; $p < 0.05$; Table 4). Comparison of the feeder: nonfeeder ratios of control burrow crab females (85:24) and control hording crab females (121:43) showed no significant difference between the two groups ($\chi^2 = 0.62$; $p > 0.05$; Table 5).

Analysis of variance of the foraging distances of control burrow crab males (10.3 ± 5.7 cm) and control burrow crab females (8.7 ± 5.6 cm) revealed no significant difference between the group means ($F = 0.77$; $p > 0.05$).

Visual censusing of the foraging distances of the control hording crab population at low tide provided the data presented in Table 6. Approximately 48% of the sample group (48.8% for males and 46.6% for females) was distributed within the lower one-third of the exposed beach. For both males and females, the number of crabs in the lower

TABLE 3

NUMBERS OF FEEDERS AND NONFEEDERS — CONTROL HORDING CRAB GROUP

	Feeders	Nonfeeders
Males	154 (148.67)	39 (44.33)
Females	121 (126.33)	43 (37.67)

Values in parentheses are expected frequencies.

$\chi^2 = 1.80$; d.f. = 1; $p > 0.05$.

TABLE 4

NUMBERS OF FEEDERS AND NONFEEDERS — CONTROL BURROW CRAB MALES AND CONTROL HORDING CRAB MALES

	Feeders	Nonfeeders
Male burrow crabs	239 (226.30)	23 (35.70)
Male Hording crabs	154 (166.70)	39 (26.30)

Values in parentheses are expected frequencies.

$\chi^2 = 12.33$; d.f. = 1; $p < 0.05$.

TABLE 5

NUMBERS OF FEEDERS AND NONFEEDERS — CONTROL BURROW CRAB FEMALES AND CONTROL HORDING CRAB FEMALES

	Feeders	Nonfeeders
Female burrow crabs	85 (82.25)	24 (26.75)
Female hording crabs	121 (123.75)	43 (40.25)

Values in parentheses are expected frequencies.

$\chi^2 = 0.62$; d.f. = 1; $p > 0.05$.

TABLE 6

RELATIVE BEACH POSITION OF HORDING CRABS AT LOW TIDE — CONTROL HORDING CRAB GROUP

	Males	Females
Upper beach	31 (30.70)	27 (27.30)
Middle beach	57 (59.27)	55 (52.73)
Lower beach	84 (82.03)	71 (72.97)

Values in parentheses are expected frequencies.

$\chi^2 = 0.29$; d.f. = 2; $p > 0.05$.

beach segment was significantly higher than the number of crabs in the middle or upper beach segments (χ^2 = 24.51 for males; χ^2 = 19.44 for females; $p < 0.05$). Comparison of the frequency distributions of males and females indicated no significant difference between the location of males and females on the beach slope (χ^2 = 0.29; $p > 0.05$).

B. Burrow-covering experiment

Analysis of variance of the feeding rates of previously burrow-confined (and, presumably, food-deprived) crabs revealed significant differences between the feeding rates of males (47.8 ± 9.7 movts./min.) and females (70.6 ± 12.1 movts./min.; F = 31.94; $p < 0.05$; Table 7). As in the control burrow crab and control hording crab groups, males fed at approximately 2/3 the rate of females.

Comparison of the feeding rates of males from the control burrow crab group (42.9 ± 6.9 movts./min.) with those of males from the burrow-confined group (47.8 ± 9.7 movts./min.) revealed no significant difference between the means (F = 3.88; $p > 0.05$; Table 7). Comparison of the feeding rates of females from the control burrow crab group (67.0 ± 11.8 movts./min.) with those of females from the burrow-confined group (70.6 ± 12.1 movts./min.) similarly showed no significant difference between the means (F = 0.85; $p > 0.05$; Table 7).

Analysis of variance of the foraging distances of males (9.5 ± 4.8 cm) and females (9.9 ± 5.1 cm) from the burrow-confined group revealed no significant difference between the group means (F = 0.06; $p > 0.05$; Table 8). Comparison of the foraging distances of

TABLE 7

ANALYSIS OF VARIANCE SUMMARIES FOR FEEDING RATES OF CONTROL BURROW CRABS AND PREVIOUSLY BURROW-CONFINED BURROW CRABS

Source	D.F.	S.S.	M.S.	F
Comparison of feeding rates of male control burrow crabs and male burrow-confined burrow crabs.				
Between groups	1	246.26	246.26	3.88
Within groups	44	2794.57	63.51	
Total	45	3040.83		
Comparison of feeding rates of female control burrow crabs and female burrow-confined burrow crabs.				
Between groups	1	120.42	120.42	0.85
Within groups	40	5637.50	140.94	
Total	41	5757.92		
Comparison of feeding rates of male and female control burrow crabs.				
Between groups	1	8530.79	8530.79	92.36*
Within groups	57	5264.70	92.36	
Total	58	13795.49		
Comparison of feeding rates of male and female burrow-confined burrow crabs.				
Between groups	1	3747.25	3747.25	31.94*
Within groups	27	3167.37	117.31	
Total	28	6914.62		

*Significant at the 0.05 level.

TABLE 8

ANALYSIS OF VARIANCE SUMMARIES FOR FORAGING DISTANCES OF CONTROL BURROW CRABS AND PREVIOUSLY BURROW-CONFINED BURROW CRABS

Source	D.F.	S.S.	M.S.	F
Comparison of foraging distances of male and female control burrow crabs.				
Between groups	1	24.80	24.80	0.77
Within groups	38	1231.44	32.41	
Total	39	1256.24		
Comparison of foraging distances of male and female burrow-confined crabs.				
Between groups	1	1.41	1.41	0.06
Within groups	28	682.93	24.39	
Total	29	684.34		
Comparison of foraging distances of male control burrow crabs and male burrow-confined crabs.				
Between groups	1	5.49	5.49	0.19
Within groups	33	945.20	28.64	
Total	34	950.69		
Comparison of foraging distances of female control burrow crabs and female burrow-confined crabs.				
Between groups	1	12.52	12.52	0.43
Within groups	33	969.17	29.37	
Total	34	981.69		

male crabs from the control burrow crab group (10.3 ± 5.7 cm) with those of male crabs from the burrow-confined group (9.5 ± 4.8 cm) showed that there was no significant difference between the group means ($F = 0.19$; $p > 0.05$; Table 8). Comparison of the foraging distances of female crabs from the control burrow crab group (8.7 ± 5.6 cm) with those of females from the burrow-confined group (9.9 ± 5.1 cm) revealed no significant difference between the group means ($F = 0.43$; $p > 0.05$; Table 8).

Observation of the movements of burrow crabs during the calculation of foraging distances indicated that a crab's distance from its burrow after three minutes of foraging was influenced by the crab's location prior to its retreat into the burrow. Crabs which resumed feeding after having been scared into their burrows usually moved quickly to the spot at which they were last feeding, traveling down shallow furrows in the sand which radiated outward from the burrow entrances. Further observation revealed that these furrows were created by the crabs themselves during the course of their foraging activities.

Contingency table analysis of feeder:nonfeeder ratios for previously burrow-confined crabs (52:1) and control burrow crabs (324:47) revealed that the burrow-confined group had a significantly larger percentage of feeders ($\chi^2 = 5.37$; $p < 0.05$; Table 9). Within the previously burrow-confined group, the feeder:nonfeeder ratio of males (35:0) was much greater than that of females (17:1). Because of the extremely low expected numbers of nonfeeding crabs in both of these subgroups, however, the feeder:nonfeeder ratios could not be compared by chi-square analysis (Sokal and Rohlf, 1969).

TABLE 9

NUMBERS OF FEEDERS AND NONFEEDERS — CONTROL BURROW CRABS AND PREVIOUSLY BURROW-CONFINED BURROW CRABS

	Feeders	Nonfeeders
Control burrow crabs	324 (329)	47 (42)
Confined burrow crabs	52 (47)	1 (6)

Values in parentheses are expected frequencies.

$\chi^2 = 5.37$; d.f. = 1; $p < 0.05$.

C. Burrow crab enclosure experiment

Feeding rates were calculated for the crabs in each of the four enclosures in this experiment. In the enriched sand enclosures, these rates were as follows: 42.5 ± 6.2 movts./min. for starved males; 67.7 ± 6.1 movts./min. for starved females; 41.5 ± 5.7 movts./min. for fed males; and 63.7 ± 7.5 movts./min. for fed females. In the enriched sand enclosures, the feeding rates were: 42.1 ± 6.1 movts./min. for starved males; 66.0 ± 6.4 movts./min. for starved females; 40.7 ± 5.1 movts./min. for fed males; and 64.8 ± 5.5 movts./min. for fed females.

Analysis of variance of feeding rates for the four groups of male crabs in this experiment yielded an F value of 0.19, indicating that there were no significant differences between the male group means ($p > 0.05$). An ANOVA of feeding rates for the four groups of female crabs produced a similar nonsignificant F value of 0.71 ($p > 0.05$). Differences between the feeding rates of males and females within each of the enclosures were found to be highly significant, however. Table 10 summarizes the ANOVA tests for feeding rates of the experimental groups.

Because the four enclosures in this experiment contained equal numbers of crabs, the number of feeding crabs (or crabs on the sand surface) in each enclosure can be compared directly, without using ratio notation. Contingency table analysis of the frequency distributions of feeders and nonfeeders in the four burrow crab enclosures revealed that the two starved crab groups had a significantly higher number of feeders (40) than did the fed crab groups (25; $\chi^2 = 7.89$;

TABLE 10

ANALYSIS OF VARIANCE SUMMARIES FOR FEEDING RATES OF BURROW CRABS — BURROW CRAB ENCLOSURE EXPERIMENT

Source	D.F.	S.S.	M.S.	F
Comparison of feeding rates of all male burrow crab groups.				
Between groups	3	19.39	6.49	0.19
Within groups	36	1212.64	33.68	
Total	39	1232.03		
Comparison of feeding rates of all female burrow crab groups.				
Between groups	3	87.70	29.23	0.71
Within groups	36	1479.92	41.11	
Total	39	1567.62		
Comparison of feeding rates of starved males and starved females, both on enriched sand.				
Between groups	1	3170.16	3170.16	83.25*
Within groups	18	685.52	38.08	
Total	19	3855.68		
Comparison of feeding rates of fed males and fed females, both on enriched sand.				
Between groups	1	2470.87	2470.87	55.58*
Within groups	18	800.26	44.46	
Total	19	3271.13		
Comparison of feeding rates of starved males and starved females, both on unenriched sand.				
Between groups	1	2848.89	2848.89	73.44*
Within groups	18	698.17	38.79	
Total	19	3547.06		
Comparison of feeding rates of fed males and fed females, both on unenriched sand.				
Between groups	1	2904.05	2904.05	102.76*
Within groups	18	508.61	28.26	
Total	19	3412.66		

*Significant at the 0.05 level.

$p < 0.05$; Table 11). No significant difference was found between the two starved crab groups, or between the two fed crab groups, in this respect.

Comparison of the number of crabs on the sand surface and crabs in burrows for each of the four burrow crab enclosures revealed that the two starved crab groups had a significantly higher number of surface-active crabs one hour after release (43) than did the two fed crab groups (19; $\chi^2 = 22.54$; $p < 0.05$; Table 12). Comparison of the two starved crab groups revealed that the starved crabs on enriched sand had a significantly higher number of surface-active crabs (25) than did the starved crabs on unenriched sand (18; $\chi^2 = 4.02$; $p < 0.05$). No significant difference was found between the two fed crab groups in this respect.

D. Hording crab enclosure experiment

Feeding rates were calculated for hording crabs in each of the enclosures in this experiment. In the enriched sand enclosures, these rates were as follows: 42.3 ± 5.7 movts./min. for starved males; 69.2 ± 5.9 movts./min. for starved females; 41.2 ± 6.3 movts./min. for fed males; and 65.7 ± 5.0 movts./min. for fed females. In the unenriched sand enclosures, the feeding rates were: 42.4 ± 5.6 movts./min. for starved males; 65.2 ± 7.8 movts./min. for starved females; 40.7 ± 5.5 movts./min. for fed males; and 64.9 ± 6.1 movts./min. for fed females.

Analysis of variance of feeding rates for the four groups of male crabs indicated that there were no significant differences between the

TABLE 11

NUMBERS OF FEEDERS AND NONFEEDERS — BURROW CRAB ENCLOSURE EXPERIMENT

	Feeders	Nonfeeders
Starved crabs on enriched sand	21 (16.25)	9 (13.75)
Fed crabs on enriched sand	12 (16.25)	18 (13.75)
Starved crabs on unenriched sand	19 (16.25)	11 (13.75)
Fed crabs on unenriched sand	13 (16.25)	17 (13.75)

Values in parentheses are expected frequencies.

$\chi^2 = 7.89$; d.f. = 3; $p < 0.05$.

TABLE 12

NUMBERS OF CRABS ON THE SAND SURFACE AND CRABS IN BURROWS — BURROW CRAB ENCLOSURE EXPERIMENT

	Crabs on the Sand Surface	Crabs in Burrows
Starved crabs on enriched sand	25 (15.5)	5 (14.5)
Fed crabs on enriched sand	9 (15.5)	21 (14.5)
Starved crabs on unenriched sand	18 (15.5)	12 (14.5)
Fed crabs on unenriched sand	10 (15.5)	20 (14.5)

Values in parentheses are expected frequencies.

$\chi^2 = 22.54$; d.f. = 3; $p < 0.05$.

male group means ($F = 0.20$; $p > 0.05$). An ANOVA of feeding rates for the four groups of female crabs similarly showed no significant differences between the female group means ($F = 1.13$; $p > 0.05$). Differences between the feeding rates of males and females in each of the enclosures were found to be highly significant, however. Table 13 summarizes these ANOVA tests.

Because the four enclosures in this experiment contained equal numbers of crabs, the number of feeding crabs (or crabs on the sand surface, or crabs within 60 cm of the water) in each enclosure can be compared directly. Contingency table analysis of the numbers of feeders and nonfeeders in each of the four enclosures showed that the two starved crab groups had a significantly higher number of feeders (157) than did the two fed crab groups (38; $\chi^2 = 126.12$; $p < 0.05$; Table 14). Comparison of the two fed crab groups revealed that fed crabs on enriched sand had a significantly higher number of feeders (26) than did fed crabs on unenriched sand (12; $\chi^2 = 6.13$; $p < 0.05$). No significant difference was found between the two starved crab groups in this respect.

Contingency table analysis of the relative position of hording crabs on the intertidal beach slope showed that the two starved crab groups had a significantly greater number of crabs located within 60 cm of the water's edge, and therefore farther from the burrows, (74) than did the fed crab groups (6; $\chi^2 = 70.62$; $p < 0.05$; Table 15).

Contingency table analysis of the numbers of crabs on the sand surface and crabs in burrows in each of the four hording crab enclosures revealed that the two starved crab groups had a significantly higher

TABLE 13

ANALYSIS OF VARIANCE SUMMARIES FOR FEEDING RATES OF HORDING CRABS — HORDING CRAB ENCLOSURE EXPERIMENT

Source	D.F.	S.S.	M.S.	F
Comparison of feeding rates of all male hording crab groups.				
Between groups	3	20.01	6.67	0.20
Within within	36	1171.97	32.55	
Total	39	1191.98		
Comparison of feeding rates of all female hording crab groups.				
Between groups	3	122.18	40.73	1.13
Within groups	36	1293.93	35.94	
Total	39	1416.11		
Comparison of feeding rates of starved males and starved females, both on enriched sand.				
Between groups	1	3639.60	3639.60	107.55*
Within groups	18	609.19	33.84	
Total	19	4248.79		
Comparison of feeding rates of fed males and fed females, both on enriched sand.				
Between groups	1	2979.24	2979.24	96.63*
Within groups	18	554.89	30.83	
Total	19	3534.13		
Comparison of feeding rates of starved males and starved females, both on unenriched sand.				
Between groups	1	2580.99	2580.99	67.25*
Within groups	18	690.89	38.38	
Total	19	3271.88		
Comparison of feeding rates of fed males and fed females, both on unenriched sand.				
Between groups	1	2928.20	2928.20	86.28*
Within groups	18	610.93	33.94	
Total	19	3539.13		

*Significant at the 0.05 level.

TABLE 14

NUMBERS OF FEEDERS AND NONFEEDERS — HORDING CRAB ENCLOSURE EXPERIMENT

	Feeders	Nonfeeders
Starved crabs on enriched sand	81 (48.75)	39 (71.25)
Fed crabs on enriched sand	26 (48.75)	94 (71.25)
Starved crabs on unenriched sand	76 (48.75)	44 (71.25)
Fed crabs on unenriched sand	12 (48.75)	108 (71.25)

Values in parentheses are expected frequencies.

$\chi^2 = 126.12$; d.f. = 3; $p < 0.05$.

TABLE 15

RELATIVE BEACH POSITION OF HORDING CRABS — HORDING CRAB ENCLOSURE EXPERIMENT

	Number of Crabs Within 60 cm of Water	Number of Crabs > 60 cm from Water
Starved crabs on enriched sand	42 (20)	108 (130)
Fed crabs on enriched sand	6 (20)	144 (130)
Starved crabs on unenriched sand	32 (20)	118 (130)
Fed crabs on unenriched sand	0 (20)	150 (130)

Values in parentheses are expected frequencies.

$\chi^2 = 70.62$; d.f. = 3; $p < 0.05$.

number of surface-active crabs one hour after release (218) than did the fed crab groups (143; $\chi^2 = 65.91$; $p < 0.05$; Table 16). No significant difference was found between the two starved crab groups, or between the two fed crab groups, in this respect.

Substrate Food Distribution and Field Extraction Efficiencies

Results of the quantitative organic carbon analysis of substrate and feeding pellet samples are shown in Table 17. The average organic carbon content for all substrate samples was 0.169% ± 0.053. Analysis of variance of the organic carbon levels of all soil samples from the supratidal sand flat (0.152% ± 0.043) and intertidal beach slope (0.199% ± 0.056) showed that substrate from the latter area had significantly higher levels of organic carbon ($F = 10.65$; $p < 0.05$; Table 18). Analysis of variance of the organic carbon content of substrate in the uppermost intertidal beach transect, transect F (0.147% ± 0.017), and the lower-most intertidal beach transect, transect H (0.244% ± 0.055) revealed that the organic carbon content of the lower-beach transect was significantly higher ($F = 17.50$; $p < 0.05$; Table 18).

The average organic carbon content for all feeding pellet samples was 0.148% ± 0.043. Analysis of variance of all substrate and feeding pellet samples showed that the feeding pellet samples had significantly lower levels of organic carbon ($F = 4.70$; $p < 0.05$; Table 18). The difference between the mean values for all substrate samples (0.169%)

TABLE 16

NUMBERS OF CRABS ON THE SAND SURFACE AND CRABS IN BURROWS — HORDING CRAB ENCLOSURE EXPERIMENT

	Crabs on the Sand Surface	Crabs in Burrows
Starved crabs on enriched sand	111 (90.25)	9 (29.75)
Fed crabs on enriched sand	77 (90.25)	43 (29.75)
Starved crabs on unenriched sand	107 (90.25)	13 (29.75)
Fed crabs on unenriched sand	66 (90.25)	54 (29.75)

Values in parentheses are expected frequencies.

$\chi^2 = 65.91$; d.f. = 3; $p < 0.05$.

TABLE 17

PERCENT ORGANIC CARBON BY DRY WEIGHT FOR UNFORAGED SUBSTRATE AND FEEDING PELLET SAMPLES IN THE BURROW CRAB AND HORDING CRAB AREAS

Site	Percent Organic Carbon by Dry Wt.	
	Unforaged Substrate	Feeding Pellets
Supratidal sand flat (burrow crab area) transects		
A1	.161	.166
A2	.193	.156
A3	.133	.133
A4	.156	.135
A5	.200	.193
A6	.192	.172
Transect mean	.172 ± .027	.159 ± .023
B1	.169	.150
B2	.146	.183
B3	.135	.095
B4	.138	.127
B5	.123	.109
B6	.116	.105
Transect mean	.138 ± .019	.128 ± .033
C1	.117	.111
C2	.095	.073
C3	.108	.089
C4	.095	.088
C5	.095	.064
C6	.102	.079
Transect mean	.102 ± .009	.084 ± .016
D1	.137	.192
D2	.272	.218
D3	.144	.157
D4	.190	.166
D5	.216	.143
D6	.183	.150
Transect mean	.190 ± .050	.171 ± .029

TABLE 17 (Continued)

Site	Percent Organic Carbon by Dry Wt.	
	Unforaged Substrate	Feeding Pellets
E1	.172	.150
E2	.187	.166
E3	.178	.122
E4	.117	.062
E5	.187	.139
E6	.091	.112
Transect mean	.155 ± .041	.125 ± .036
Intertidal beach (hording crab area) transects		
F1	.157	.160
F2	.112	.142
F3	.147	.137
F4	.157	.147
F5	.152	.125
F6	.155	.145
Transect mean	.147 ± .017	.143 ± .012
G1	.189	.169
G2	.283	.244
G3	.197	.221
G4	.174	.125
G5	.200	.155
G6	.188	.166
Transect mean	.205 ± .039	.180 ± .044
H1	.234	.219
H2	.257	.202
H3	.162	.167
H4	.212	.162
H5	.274	.207
H6	.324	.197
Transect mean	.244 ± .055	.192 ± .023

TABLE 18

ANALYSIS OF VARIANCE SUMMARIES FOR ORGANIC CARBON CONTENT OF UNFORAGED SUBSTRATE AND FEEDING PELLETS

Source	D.F.	S.S.	M.S.	F
Comparison of organic carbon content of unforaged substrate and feeding pellets (all samples).				
Between groups	1	0.011	0.011	4.70*
Within groups	94	0.220	0.002	
Total	95	0.231		
Comparison of organic carbon content of substrate samples from burrow crab area and hording crab area.				
Between groups	1	0.025	0.025	10.65*
Within groups	46	0.108	0.002	
Total	47	0.133		
Comparison of organic carbon content of substrates from transect F (upper-beach) and transect H (lower-beach).				
Between groups	1	0.007	0.007	17.50*
Within groups	10	0.004	0.0004	
Total	11	0.011		

*Significant at the 0.05 level.

and all feeding pellet samples (0.148%) represents a 12.4% reduction in organic carbon content from unforaged substrate to feeding pellets. Mean extraction efficiencies for crabs on the supratidal sand flat and intertidal beach slope, respectively, were 11.8% and 13.6%.

Laboratory Experiments

A. Feeding choice experiment

Data from the feeding choice experiment are summarized in Table 19, Figure 2, and Table 20. Linear regression of the weights of feeding pellets produced by crabs feeding at different levels of substrate enrichment revealed a significant positive correlation between substrate food level (expressed as a log transformation of percent organic carbon) and weight of feeding pellets produced on the substrate (correlation coefficient, r, = .95 for starved crabs; r = .91 for fed crabs). The lowest weights of feeding pellets were produced at the lowest levels of substrate enrichment, and the highest feeding pellet weights were found at the highest enrichment levels. This trend is indicated in Table 19 and Figure 2.

The results of this experiment demonstrated that both starved and fed crabs could distinguish between enriched and unenriched sand, even at enrichment levels of 0.01%. In every feeding choice trial, more feeding pellets were produced on the enriched sand than on the unenriched sand. At all enrichment levels, starved crabs produced a greater amount of feeding pellets than did fed crabs (Table 19, Figure 2).

TABLE 19

AVERAGE WEIGHTS OF FEEDING PELLETS PRODUCED IN ONE HOUR BY SIX CRABS FORAGING ON ENRICHED AND UNENRICHED SAND — FEEDING CHOICE EXPERIMENT

Enrichment Level	Crab Group	Average Dry Weight (g) of Feeding Pellets Produced by Six Crabs Foraging for One Hour	
		Unenriched Sand	Enriched Sand
0.01%	Starved Crabs	3.56 ± 0.90	9.19 ± 1.45
	Fed Crabs	1.19 ± 1.18	2.33 ± 1.77
0.05%	Starved Crabs	4.52 ± 1.14	37.42 ± 3.69
	Fed Crabs	2.28 ± 1.10	6.60 ± 4.45
0.10%	Starved Crabs	5.90 ± 1.08	44.59 ± 5.09
	Fed Crabs	3.37 ± 1.39	17.18 ± 3.30
0.50%	Starved Crabs	5.03 ± 0.87	51.90 ± 6.51
	Fed Crabs	4.40 ± 1.07	18.30 ± 6.44

Tabled values are means plus or minus one standard deviation.

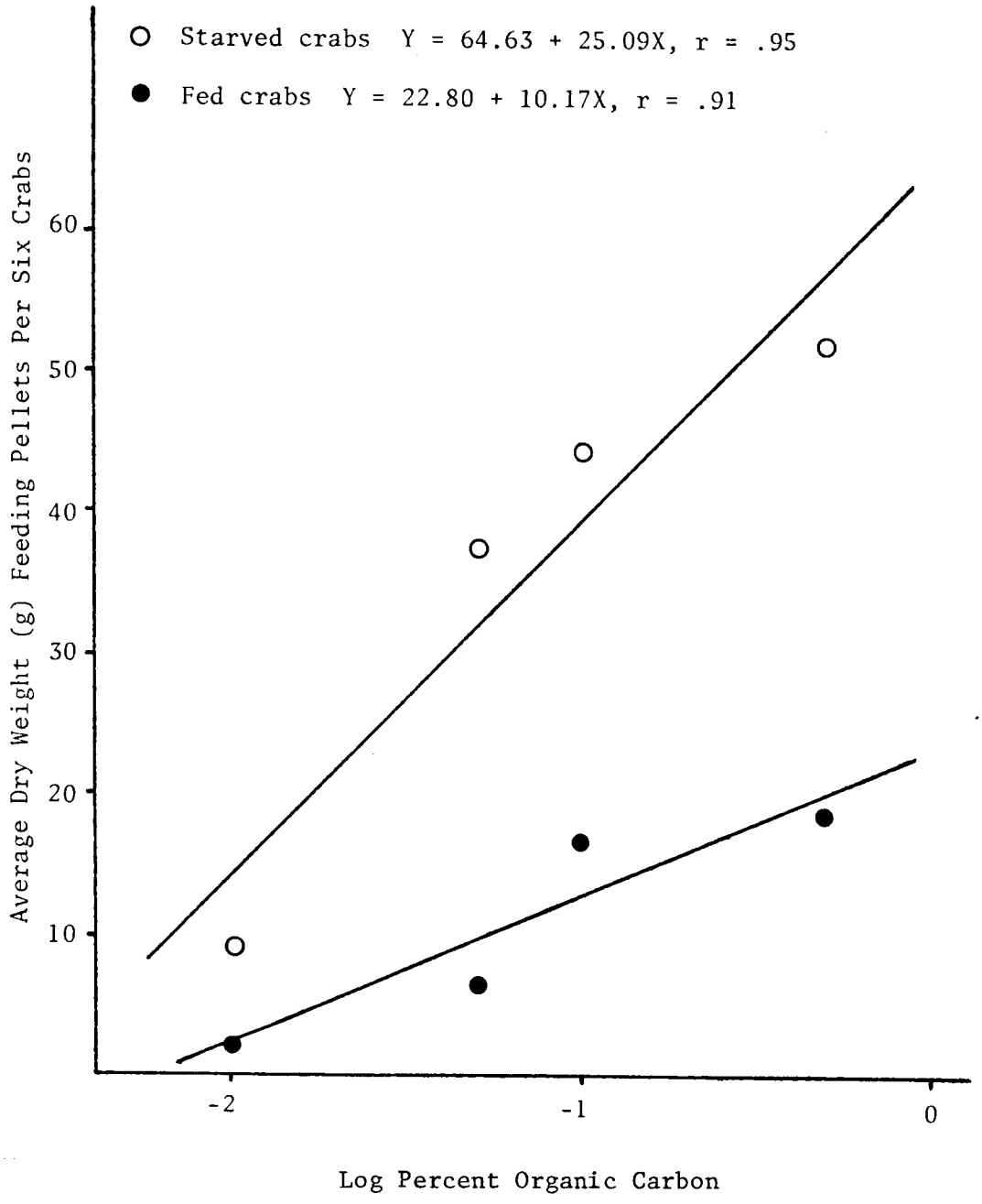

Figure 2. Average dry weight of feeding pellets per six crabs versus $\log_{10}$ percent organic carbon of sand, for starved and fed crabs.

TABLE 20

EXTRACTION EFFICIENCIES FOR CRABS FEEDING ON ENRICHED SAND — FEEDING CHOICE EXPERIMENT

Enrichment Level	% Organic Carbon, Unforaged Sand	% Organic Carbon, Feeding Pellets	Extraction Efficiency
0.00%	0.034	0.049	- [1]
0.01%	0.043	0.042	2.3%
0.05%	0.076	0.054	28.9%
0.10%	0.122	0.065	46.7%
0.50%	0.465	0.124	73.3%

[1]Since the organic carbon content of the feeding pellets was higher than that of the unprocessed sand in this case, no extraction efficiency could be calculated. See text for further explanation.

The two regression lines shown in Figure 2 were tested at the 0.05 significance level for parallelism, using a small-sample t-test (Sokal and Rohlf, 1969). The calculated t value (2.37) from this test revealed that the slope of the regression line for starved crabs was significantly steeper than the regression line for fed crabs. This indicates that, although both starved and fed crabs increased their production of feeding pellets in response to increases in food density, the rate of increase in feeding pellet production was significantly greater for starved crabs.

Table 20 shows the mean organic carbon levels for each of the unforaged substrates, and for feeding pellets derived from these substrates. Average extraction efficiencies for each level of enrichment are also shown. As indicated in the table, extraction efficiencies varied considerably between enrichment levels. Note that the organic carbon content for feeding pellets found on the unenriched sand portion of the tanks is higher than the organic carbon content of the unenriched substrate. This indicates that some of the feeding pellets found on the unenriched substrate were actually derived from the enriched substrate in the other half of the experimental tank. Supporting evidence for this conclusion is provided by the fact that the majority of the feeding pellets found on the unenriched substrate were within 4 cm of the plastic partition which separated the enriched and unenriched substrates. In addition, the average weights of feeding pellets found on unenriched sand increased as the enrichment level of adjacent substrates was increased (Table 19).

Brief observation of the feeding behavior of crabs in this experiment revealed that at the highest levels of substrate enrichment (0.5% and 0.1%), crabs sometimes foraged on feeding pellets. This behavior was not observed at enrichment levels of 0.05% and 0.01%.

B. Feeding claw amputation experiment

Average feeding rates for the three crab groups in this experiment were: 60.6 ± 7.4 movts./min. for the control group; 62.7 ± 8.4 movts./min. for the ambulatory leg amputee group; and 41.8 ± 6.8 movts./min. for the feeding claw amputee group. Feeding claw amputees fed at 69% the rate of the control group, and at 67% the rate of the ambulatory leg amputee group. Control crabs fed at 97% the rate of the ambulatory leg amputees.

Analysis of variance of the feeding rates of the three crab groups in this experiment (Table 21) revealed that the control group fed significantly faster than the feeding claw amputee group ($F = 193.61$; $p < 0.05$); the ambulatory leg amputee group also fed significantly faster than the feeding claw amputee group ($F = 168.28$; $p < 0.05$). No significant difference was found between the feeding rates of the control group and the ambulatory leg amputee group, however ($F = 0.54$; $p > 0.05$).

An analysis of variance comparison of the feeding rates of the control group and ambulatory leg amputee group with those of 60 randomly-selected females from the field experiments revealed no significant differences between the three group means ($F = 0.94$; $p > 0.05$). An analysis of variance comparison of the feeding rates of the (female)

TABLE 21

ANALYSIS OF VARIANCE SUMMARIES FOR FEEDING RATES OF FEMALE CRABS — FEEDING CLAW AMPUTATION EXPERIMENT

Source	D.F.	S.S.	M.S.	F.
Comparison of feeding rates of control group and feeding claw amputee group.				
Between groups	1	12964.24	12964.24	193.61*
Within groups	178	11919.43	66.96	
Total	179	24883.67		
Comparison of feeding rates of control group and ambulatory leg amputee group.				
Between groups	1	63.73	63.73	0.54
Within groups	178	20826.63	117.00	
Total	179	20890.36		
Comparison of feeding rates of feeding claw amputee group and ambulatory leg amputee group.				
Between groups	1	14845.81	14845.81	168.28*
Within groups	178	15702.76	88.22	
Total	179	30548.57		

*Significant at the 0.05 level.

feeding claw amputee group with those of 60 randomly-chosen males from the field experiments revealed no significant difference between the means ($F = 0.67$; $p > 0.05$).

Contingency table analysis of feeder:nonfeeder ratios at one-half hour after release for each of the crab groups in this experiment revealed no significant differences between the frequency distributions of the three groups ($\chi^2 = 0.96$; $p > 0.05$; Table 22). Comparison of feeder:nonfeeder ratios at each of the other observation intervals (one, two, and three hours after release) produced chi-square values of 0.84, 1.28, and 1.62, respectively ($p > 0.05$; Table 22). Thus, no significant differences were found between the feeder:nonfeeder ratios of the three crab groups at any of the observation intervals.

Contingency table analysis of the ratios of crabs on the sand surface to crabs in burrows for the three experimental groups revealed no significant differences between the frequency distributions of the groups ($\chi^2 = 0.50$; $p > 0.05$; Table 23).

TABLE 22

SUMMARY OF CONTINGENCY TABLE ANALYSES OF FEEDER:NONFEEDER RATIOS — FEEDING CLAW AMPUTATION EXPERIMENT

Time After Release	χ^2 Value[1]	S/NS[2]
1/2 hour	0.96	ns
1 hour	0.84	ns
2 hours	1.28	ns
3 hours	1.62	ns

[1] χ^2 values are derived from contingency table analysis of the frequency distributions of feeders and nonfeeders in the three experimental groups (control crabs, feeding claw amputees, and ambulatory leg amputees) at each observation interval.

[2] S/NS = significance or nonsignificance at the 0.05 level.

TABLE 23

NUMBERS OF CRABS ON THE SAND SURFACE AND CRABS IN BURROWS — FEEDING CLAW AMPUTATION EXPERIMENT

	Crabs on the Sand Surface	Crabs in Burrows
Control group	33 (33.67)	7 (6.33)
Feeding claw amputees	33 (33.67)	7 (6.33)
Ambulatory leg amputees	35 (33.67)	5 (6.33)

Values in parentheses are expected frequencies.

$\chi^2 = 0.50$; d.f. = 2; $p > 0.05$.

V. DISCUSSION

In this study, feeding rates for each of the sexes of sand fiddler crabs did not vary significantly across any of the experimental groups; between-sex differences in feeding rates were significant in all of the experimental groups, however. This illustrates the influence of sexual dimorphism on the feeding rates of *Uca pugilator*. In every experiment involving feeding rates, males fed at approximately 2/3 the rate of females, not half as fast, as reported for *U. pugnax* (Valiela et al., 1974). Especially interesting is the finding that female crabs with only one feeding claw feed at 2/3 the rate of females with two feeding claws, and at approximately the same rate as normal males. This indicates that female crabs with one feeding claw increase the rate of movement of the remaining claw, thereby partially compensating for their relative disadvantage.

It is probable that differences in the feeding rates of males and females are due primarily to the fact that males have only one feeding claw, and not to major differences in assimilation efficiencies or metabolic demands. Valiela et al. (1974) found no differences in the respiratory rates of male and female *U. pugnax* individuals of comparable sizes; in addition, they found that food intake, fecal pellet production, and assimilation efficiencies were quite similar for males and females.

In order to avoid predation, dessication, and thermal stress, and to ensure adequate food intake each day, it would seem advantageous for sand fiddler crabs to feed as rapidly as possible. Maximization of the rate of ingestion would mean that a minimum of the daily activity period

would be relegated to feeding behavior, and more time would remain for burrow maintenance, courtship, territorial defense, predator avoidance, and other important activities. In the present study, males and females fed at fairly constant rates while they were in a feeding mode of behavior, indicating that both sexes may have been feeding at or near their maximum rates under the existing environmental conditions. Since females with two feeding claws fed at a rate 1.5 times that of males (and females with one feeding claw), and not twice as fast, the rate-limiting step in their feeding operation may be the flotation sorting process. For males (and females with one feeding claw), the rate-limiting step may be the substrate-to-mouth movement of the feeding claw.

Feeding rates for *U. pugilator* in this study were approximately twice as high as those calculated for *U. pugnax* by Valiela et al. (1974). The considerable discrepancy between the feeding rates of the two species may be due to temperature regime dissimilarities, age differences between the experimental subjects, inequalities in substrate food availability, or inherent genetic differences. The feeding rates for *U. pugnax* were calculated entirely from laboratory observations, however, making it difficult to estimate the validity or causation of these interspecific differences in feeding rates.

Feeder:nonfeeder ratios provide an estimate of the portion of the observable crab population that is feeding at any given time. Calculated over an entire daily activity period, feeder:nonfeeder ratios give an indication of the relative lengths of the daily foraging periods of population subgroups. In this study, feeder:nonfeeder ratios varied

according to differences in the food deprivation levels of crabs, and to a lesser extent, according to differences in substrate food availability. This was demonstrated in the results of the burrow crab and hording crab enclosure experiments. In both experiments, the starved crab groups had significantly higher numbers of feeders than the fed crab groups. Apparently, food satiation switches sand fiddlers from a feeding to a nonfeeding mode of behavior, instead of gradually slowing their feeding rates. On the other hand, an abundance of food in the substrate may result in higher numbers of feeders, even in crabs which are relatively highly satiated. In the hording crab enclosure experiment, fed crabs on enriched sand had significantly more feeders than did fed crabs on unenriched sand. The two fed crab groups in the burrow crab enclosure experiment did not vary significantly in this regard, however.

The comparison of feeder:nonfeeder ratios of the previously burrow-confined burrow crabs and the control burrow crabs revealed significantly higher numbers of feeders among crabs which had been confined to their burrows for 48 hours. This indicates that sand fiddlers may do less, if any, feeding while they are in their burrows. Laboratory-based studies of the underground activities of *U. pugilator* would be invaluable in providing further information in this area.

Among the two field experiment control groups, burrow crabs had a significantly higher proportion of feeders than hording crabs. One might expect the opposite to be true, since hording crabs have less time each day to feed on the intertidal slopes than do the burrow crabs,

which live in a supratidal area. In addition, since hording crabs feed at greater distances from their burrows, it is possible that they are in greater danger of predation while feeding than are the burrow crabs. If this were indeed the case (which it may not be), then higher feeder: nonfeeder ratios among hording crabs might again be expected.

Comparison of the organic carbon content of substrates in the burrow crab and hording crab areas provides one possible explanation for the disparate feeder:nonfeeder ratios of the two groups. Higher feeder: nonfeeder ratios among burrow crabs may be related to the lower organic carbon levels of the supratidal sand flat area. Because they live in an area of lower food density, burrow crabs may have to spend more time feeding each day to obtain an amount of food equivalent to that ingested by hording crabs on the intertidal beach slope.

In the burrow crab control group, males had significantly higher feeder:nonfeeder ratios than females. This finding corroborates the observations of Valiela et al. (1974), indicating that male fiddler crabs feed for longer periods than do females, thereby compensating behaviorally for their slower feeding rate. Although the differences between the feeder:nonfeeder ratios of male and female crabs in the hording crab control groups and the previously burrow-confined burrow crab group were not statistically significant, they indicate a similar trend.

Ratios of crabs on the sand surface to crabs in burrows provide an estimation of the relative lengths of the surface-active periods of population subgroups. In this study, these ratios were found to vary

according to differences in food deprivation and substrate food availability. One might expect that, if the danger of predation, dessication, and thermal stress were great for crabs on the sand surface and minimal for crabs in burrows, satiated crabs would tend to enter their burrows earlier than hungry crabs. This assumption appears to be supported by the results of the burrow crab and hording crab enclosure experiments. In both of these experiments, the starved crab groups had significantly higher numbers of surface-active crabs one hour after release than the fed groups; in addition, starved burrow crabs on enriched sand had significantly more surface-active crabs than did starved crabs on unenriched sand. Although the frequency distributions of surface-active crabs and crabs in burrows did not vary significantly between the two starved crab groups in the hording crab experiment, they indicate a similar trend.

Differences in the behavior of fed and starved crabs were especially noticeable in the hording crab enclosure experiment. In this experiment, the majority of the fed crabs crowded against the upslope end of the enclosure, many of them digging burrows in the sand. Most of the starved crabs, on the other hand, moved toward the lower end of the enclosure and remained on the sand surface, feeding.

The similarity of the ratios of surface-active crabs:crabs in burrows for each of the three groups in the feeding claw amputation experiment may perhaps be attributable to changes in the behavior of the amputee groups due to the amputation process. It is possible that crabs which have been recently injured tend to spend less time exposed

to the harsh environmental conditions of the substrate surface. This tendency would offset any trend toward longer foraging periods in the amputee groups.

The foraging activities of burrow crabs create shallow furrows in the substrate surrounding the burrows; these furrows radiate outward from the burrow entrances in several different directions. In this study, a burrow crab which recommenced foraging behavior after having been scared into its burrow usually traveled quickly to the site at which it was last feeding, walking down the center of one of the furrows. The crabs performing this behavior may have been responding to textural substrate cues, or they may have been responding to differences in the substrate food levels between foraged and unforaged areas. The distance of a crab from its burrow after three minutes of foraging was apparently influenced by the crab's location prior to its retreat into the burrow, and may have been indirectly related to the heterogeneity of food distribution in the burrow crab area.

The results of the hording crab enclosure experiment indicated that food deprivation levels may influence the relative positions of hording crabs on the intertidal beach slope. Significantly more starved crabs moved downslope toward the water to feed than did the fed crabs. Observation of the control hording crab group revealed that the lower beach zone contained the largest portion of the population sample. The aggregation of hording crabs near the water's edge may be directed by the crabs' requirements for moisture, both in the feeding process and in thermoregulation (Teal, 1959; Miller, 1961; Bliss, 1968; Miller and

Vernberg, 1968). The fact that the organic carbon content of the intertidal beach substrate increases downslope indicates that hording crabs may also aggregate near the water in order to obtain more food. It is possible that starved crabs are more intolerant of dessication than fed crabs, though this study provides no evidence to confirm this possibility.

Levels of organic carbon in the upper substrate of the study site averaged less than 0.2%; in comparison, substrates from Valiela et al.'s study site averaged 23.7% organic carbon by weight. As mentioned above, this difference in food availability may provide one explanation for the discrepancy between the feeding rates of *U. pugnax* and *U. pugilator*.

Uca pugilator is reportedly quite active at night in many parts of its range; in addition to nocturnal courtship behavior, hording and feeding have been observed in sand fiddler populations at night (Burkenroad, 1947; Salmon, 1965). Teal (1958) observed that the high temperatures and dessication rates associated with the exposed, barren habitat of *U. pugilator* often prevent crabs from feeding sufficiently by day. The sand fiddler's nocturnal feeding activity may therefore be due both to low food availability and to metabolically-stressful environmental conditions in the daytime. Since no observations were made at night in this study, the proportion of feeding activity occurring at night is unknown.

In the present study, the average organic carbon content of substrate from the intertidal beach was significantly higher than that of substrate from the supratidal sand flat. This finding agrees well

with those of Robertson et al. (1980), who observed that levels of chlorophyll a in the intertidal beach zone were nearly three times as high as those in a nearby salt pan area.

The feeding choice experiment in this study demonstrated that sand fiddler crabs can detect the level of food in a given substrate, and can change their feeding behavior in response to small differences in the food content of two adjacent substrates. The amount of feeding pellets produced in an hour's foraging time was positively correlated with the level of food enrichment of the substrate, and crabs responded to differences in organic carbon levels as small as 0.01%. This figure is much less than the range of variation for organic carbon content of the soils in the study site. Therefore, it is quite likely that sand fiddlers constantly modify their feeding behavior in response to gradients of food density which exist in the uppermost layer of the substrate.

Results of the feeding choice experiment showed that at all substrate enrichment levels, starved crabs produced more feeding pellets than fed crabs; in addition, differences in the amount of feeding pellets produced at different levels of substrate enrichment were greater for starved crabs than for fed crabs, indicating a stronger behavioral response to food density in starved crabs. Thus, a sand fiddler's functional response to differences in food density is apparently influenced by the crab's food satiation state.

Robertson et al. (1980) have found that *U. pugilator* can solve differences in food density over distances as small as several

millimeters. They contend that the crabs' assessment of substrate food density occurs prior to the actual process of feeding, and is accomplished by probing the substrate with the minor chelae. Results of their study indicate that crabs tend to move away from previously-foraged areas, and that this behavior is based on the crabs' perception of the lowered food density in the foraged area, rather than on textural cues provided by the feeding pellets.

Results of the feeding choice experiment in the present study agree with the findings of Robertson et al. (1980) concerning the sand fiddler's ability to detect differences in food availability over small distances. As mentioned earlier, most of the feeding pellets found in the unenriched half of the experimental tank were within 4 cm of the central partition. Substrate-probing behavior was also observed in both males and females in this experiment. The hypothesis that sand fiddler crabs respond directly to substrate food density, and not to textural cues associated with feeding pellets, was also corroborated by the present study. Crabs were observed feeding on feeding pellets derived from highly-enriched substrates. This behavior was not observed at lower levels of substrate enrichment. Assessment of substrate food levels is probably facilitated by chemoreceptors on the minor chelae and ambulatory legs (H. W. Ambrose, personal communication).

The average field extraction efficiency, calculated from samples of unforaged substrate and feeding pellets at the study site, indicated that crabs removed an average of 12.4% of the total available organic carbon in the upper 5 mm of the substrate. In 9 out of 48 sample pairs,

however, the level of organic carbon in the feeding pellets was higher than that in the adjacent unforaged substrate. It is possible that these feeding pellet samples were derived from small isolated patches of high food density; it is also possible that these feeding pellet samples were contaminated with small fragments of fecal pellets. Valiela et al. (1974) found that fecal pellets of *U. pugnax* had an average organic carbon content of 32.9%, nearly 1.4 times the organic carbon content of the substrate. Given the extremely low organic carbon levels of substrates in the habitat of *U. pugilator*, even a small fecal pellet fragment in a feeding pellet sample would result in an inaccurate estimate of the organic carbon content of the sample. Since fiddler crabs defecate while they are foraging, fecal pellets are more often associated with feeding pellets than with undisturbed substrate. It is thus probable that the actual extraction efficiencies for crabs at the study site are higher than estimates calculated on the basis of the substrate and feeding pellet samples.

At comparable levels of substrate organic carbon content, laboratory extraction efficiencies on Tetramin-enriched sand were much higher than field extraction efficiencies (46.7% vs. 12.4%). This large difference in extraction efficiencies may be related to the fact that the food in the laboratory experiments (Tetramin) was qualitatively different from the food in the substrate at the field study site. In addition, since the Tetramin food was merely held between the interstitial spaces of the sand grains, it was probably easier to remove via the flotation sorting process than were the adherent organic materials (e.g., algae, bacteria, protozoans) in the natural substrate.

In the feeding choice experiment, extraction efficiencies for crabs feeding on sand enriched with Tetramin fish food increased at higher levels of substrate enrichment. Robertson et al. (1980) similarly observed that extraction efficiencies based on removal of chlorophyll a and ATP from substrates were strongly concentration-dependent at low ambient concentrations of these two compounds.

The feeding activities of fiddler crabs may greatly influence food availability in the upper layers of the soil. Although data on the ingestion rates of algae and microbes by *Uca* are lacking in the literature, it is possible that intensive foraging in an area may help to maintain algal and microbial populations in a log growth phase (Montague, 1980). The crabs' mastication of uningestable organic particles may increase the rate of decomposition of those particles, by increasing the amount of surface area available to microbes in the soil.

The foraging activities of fiddler crabs can cause extensive mechanical distrubance to the upper few millimeters of the substrate. Kraeuter (1976) estimated that this disturbance results in the aeration and turnover of the upper 5 mm of substrate at least once a year. Mechanical disturbance to the upper substrate may also help to maintain algal growth, by increasing nutrient availability, providing a more favorable aerobic environment, and creating more light-exposed surface area (Montague, 1980).

Large numbers of fecal pellets are deposited by sand fiddlers each day. Kraeuter (1976) estimated that a large *U. pugilator* individual

produces 0.10 g (dry weight) of feces each day. This amount represents 100 to 200 fecal pellets per crab per day. The fecal pellets, which are cylindrical, compact, and covered with a mucous coating, are relatively resistant to physical destruction by rainfall and tidal inundation. They are often transported by water into small depressions in the sand, where they may accumulate in great numbers (Montague, 1980). Estimates of the organic carbon content of fecal pellets for *Uca* species range from 30% to 70% (Valiela et al., 1974; Kraeuter, 1976; Montague, 1980). Considering the extremely low ambient organic carbon content of the substrates in the sand fiddler's habitat, it seems probable that the production, transportation, and eventual degradation of these pellets might greatly influence the distribution of food in the upper substrate.

The burrowing activities of fiddler crabs may also affect the production and distribution of food resources in their habitat. Burrow excavation by *U. pugnax* individuals in Little Sipawisset marsh, Massachusetts, reportedly resulted in an annual turnover of 20% to 44.5% of the upper 15 cm of substrate (Katz, 1980). In excavating their burrows, fiddler crabs transport detritus-containing sediment from the anaerobic soil zone to the surface of the substrate, and thus probably enhance nutrient availability in the upper soil layers. This increase in nutrient availability would, in turn, promote the growth of microbial and algal populations, resulting in an increase in food density for the crabs.

The burrows themselves greatly increase the aerially-exposed surface area of the substrate, allowing the oxidized zone to extend

deeper into the soil (Katz, 1980). This increased aeration of the soil may enhance the growth of vascular plants such as *Spartina alterniflora*, whose detritus contributes to the sand fiddler's food resources (Haines and Montague, 1979; Montague, 1980).

Results from this study indicate that the relative hunger states of crabs can influence not only the amount of time the crabs spend feeding on the sand surface, but also the amount of time that they are active on the sand surface. Apparently, hunger represents a major inducement for this crab's presence on the sand surface. Sand fiddlers are evidently unable to obtain sufficient quantities of food while in their burrows, and must therefore abandon the safety and environmental stability of the burrows to enter the relatively hostile environment of the substrate surface, where food is more plentiful.

The amount of time a sand fiddler crab spends out of its burrow may be of great consequence in terms of the crab's ability to avoid predation (Crane, 1975; Aspey, 1978). Major predators of sand fiddler crabs in the study area include white ibises, Wilson's plovers, semi-palmated plovers, willets, raccoons, blue crabs, and various fish. With the exception of the raccoons, these predators capture only sand fiddlers which are active on the surface of the substrate. Feeding activity therefore exposes *U. pugilator* to increased risks of predation.

As mentioned earlier, fiddler crabs on the sand surface frequently encounter environmental conditions which are thermally and osmotically unfavorable (Teal, 1958; Vernberg and Tashian, 1959; Wilkens, 1960; Bliss, 1968; Powers and Cole, 1976). High temperatures on the substrate

surface result in increased rates of evaporative water loss for sand fiddlers. Increased rates of evaporative water loss, in turn, result in internal hypersalinity and dessication of tissues. The problem of dessication is compounded for feeding crabs by water loss associated with the flotation sorting process (Miller, 1961). Feeding fiddler crabs must therefore periodically replenish their internal water supply from external sources.

For sand fiddler crabs in the sparsely-vegetated supratidal sand flat area, all social and nonsocial activities are centered around the burrows. Since no above-ground water supply is nearby, the surface-active crabs in this area counteract evaporative water loss by periodically reentering their burrows. The distance of a feeding crab from its burrow may be of great importance in terms of the crab's survival, because it determines the crab's ability to escape from an approaching predator. Since the burrows are seldom covered by water, sand fiddlers in this area are able to forage for longer periods each day than are hording crabs; however, the average organic carbon content of the substrate is less here than on the intertidal beach slope.

In the hording crab area, burrows are located in the thick *Spartina* grass and are hidden from the view of most predators. Nearly all predation, therefore, occurs on the bare intertidal slope during low tide. In this habitat, the distance of a feeding crab from its burrow may not be as important to the crab's survival as is the distance from the crab to the dense supratidal vegetation. It is also possible that the density of the hording crab group reduces the risk of predation

for individual crabs. Feeding hording crabs replenish their internal water supply by aggregating near the water's edge, periodically entering the water to a depth of 1 - 3 cm (Herrnkind, 1968a). The tidal cycle greatly limits the amount of time available for foraging on the intertidal slope; this relative disadvantage for hording crabs may be offset, however, by the higher organic carbon content of the intertidal beach substrate, especially in the lower beach zone.

Little or no research has been directed toward the ecological relationship between burrow crabs and hording crabs in *Uca pugilator*. It is possible that these two behavioral groups represent two different stages in the life cycle of the sand fiddler crab. A more likely explanation for the different "lifestyles" of these two groups, however, may be that burrow crabs and hording crabs represent two behavioral extremes in a species whose behavioral lability allows individuals to adjust their social and nonsocial activities to different habitat types. Further research into this area is clearly needed in order to understand the full range of environmental effects on the behavior of *U. pugilator*.

Results of this study have shown that food deprivation and food availability can significantly influence the feeding behavior of *Uca pugilator*, by determining the lengths of feeding periods, and the distances traveled during feeding periods. The lengths of time that sand fiddlers feed, and their location during the feeding process, may, in turn, greatly influence the crabs' risks of predation, dessication, and hyperthermia.

Neither food deprivation nor substrate food availability significantly affected the feeding rates of *U. pugilator* in this study. Males (and females with one feeding claw) fed at approximatly 2/3 the rate of normal females in all experiments in this study, indicating that intersexual differences in feeding rates are likely a result of sexual dimorphism in this species. The constancy of feeding rates for each of the sexes may be the result of both sexes feeding as rapidly as possible, in order to maximize the rate of food ingestion.

Uca pugilator can apparently detect small differences in the food levels of adjacent substrates, and can change its feeding behavior in response to perceived food levels. The feeding activities of the sand fiddler result in a significant short-term decrease in the organic carbon levels of the foraged substrate, but the long-term effect of its feeding and burrowing activities may be an increase in the density of food in some areas. Thus, *U. pugilator* modifies its feeding behavior according to gradients of food density in its habitat, and through its foraging and burrowing activities may actually create new gradients in food density.

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