ECOLOGY OF THE GHOST CRAB *OCYPODE QUADRATA* (FABRICIUS) ON ASSATEAGUE ISLAND, MARYLAND AND THE IMPACTS OF VARIOUS HUMAN USES OF THE BEACH ON THEIR DISTRIBUTION AND ABUNDANCE

By

Edward William Christoffers III

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Zoology

1986

432-9705

ABSTRACT

ECOLOGY OF THE GHOST CRAB OCYPODE QUADRATA (FABRICIUS) ON ASSATEAGUE ISLAND, MARYLAND AND THE IMPACTS OF VARIOUS HUMAN USES OF THE BEACH ON THEIR DISTRIBUTION AND ABUNDANCE

By

Edward William Christoffers III

The purpose of this study was to investigate ghost crab, *Ocypode quadrata* (Fabricius), ecology on Assateague Island, Maryland, and to assess impacts of human uses of seashore beaches on ghost crab distribution and abundance. A two part hypothesis was formulated: 1) ghost crab ecology is similar to North Carolina and Texas populations even though the species was near the northern limit of its range, 2) human recreational use of the beach would adversely impact local ghost crab distribution and abundance.

Study sites were established in areas receiving different types and intensities of use. Transect 1 received only hiking use. Transect 2 received moderate day use and light official vehicle traffic. Transect 3 received steady off road vehicle (ORV) and individual recreational use.

Ghost crab abundance and distribution were assessed by recording burrows inside a 3 m grid along a transect from berm crest to dune toe. Burrow diameter and depth (diameter > 1.0 cm) were recorded.

Beach profiles and sand grain analyses were made at all three sites. Meterological conditions and human use intensity were measured. Availability of mole crabs, *Emerita talpoida* Say, a major prey species was also determined.

Ghost crabs were active from late April until November. Copulation occurred from June through September with new recruits arriving on the beach from May to October. Crabs appeared to be concentrated near the crest of the berm during the summer, although they were more evenly distributed than previously reported. *O. quadrata* was primarily a predator, feeding principally on *E. talpoida*.

There were no physical differences between the three sites, and prey availability and recruitment was similar. Differences in *O. quadrata* abundance between sites was attributed to human use. Abundance of *O. quadrata* was found to be statistically different between sites; transect 1 had the greatest abundance, transect 3 the lowest and transect 2, an intermediate level. ORV traffic altered the moisture content of the surface sand and prevented the crabs from establishing burrows. Human use interferred with the crabs normal diurnal activity at all sites and reduced vegetation behind the dunes at transect 2.

This Volume is Dedicated to
The Memory of My Mother

ACKNOWLEDGMENTS

I deeply appreciate the encouragement, warmth, and enthusiasm that my co-chairmen and friends, Dr. T. Wayne Porter and Dr. Robert L. Lippson provided during our association. I am just now realizing the value of the many hours they spent helping and advising me during my research.

My father, my wife Louise and children have been supportive in so many ways that I shall remain forever in their debt.

I also wish to thank my committee members, Dr. Max Hensley, Dr. Richard Snider, Dr. Donald Hall and Dr. Niles Kevern for their guidance and helpful criticism of this manuscript. In addition, I wish to thank Dr. Robert Byrne of the Virginia Institute of Marine Science, and his staff for their assistance in the analysis of sediment samples, and Mr. Kirk Starke and his crew from the Corps of Engineers for their help in the beach profiling.

My appreciation to Anne Bergman for typing the manuscript and being helpful in so many ways.

TABLE OF CONTENTS

Page

LIST OF TABLES

LIST OF FIGURES

Figure Page

INTRODUCTION

Problem:

The purpose of this study was to investigate ghost crab, Ocypode quadrata (Fabricius, 1787), population ecology on Assateague Island, Maryland, and to assess impacts of various human uses of Seashore beaches on ghost crab distribution and abundance. A two part hypothesis was formulated: 1) ghost crab ecology would be similar to that reported for North Carolina (Walcott, 1978) and Texas (Haley, 1969 and 1972; Teerling 1970) even though the species was near the northern limit of its range; and 2) human recreational use of the beach would adversely impact local ghost crab distribution and abundance.

While there have been a number of ghost crab studies (Cowles, 1908; Milne and Milne, 1946; Haley, 1969 and 1972; Letterman, 1973), only limited work has been reported concerning the population inhabiting Assateague Island (Steiner and Leatherman 1979, 1981). These studies have provided minimal information about the terrestrial life cycle of the species on Assateague Island and effects of different types and intensities of human use on their density.

Objectives:

A series of objectives were established in order to gather information about ghost crab population dynamics and ecological requirements. The following was obtained:

1) an assessment of ghost crab densities on an isolated beach, a beach utilized by bathers and a beach open to off-road vehicles (ORV);
2) an evaluation of size class distribution on the beaches, burrow location and depth;
3) an assessment of population density of a major prey species, the mole crab, *Emerita talpoida* (Say), at each of the three beach locations;
4) beach profiles and sand particle analysis;
5) an evaluation of human beach use intensity;
6) casts of various burrows within different size classes at the control beach to determine burrow construction characteristics;
7) feeding behavior, behavioral interactions, burrow maintenance activities, marking and recapture, and migratory studies at the control site only;
8) general climatic data including wind direction and velocity, air and sea temperature, tidal periodicity, barometric pressure and moon phase.

BIOLOGY OF *OCYPODE QUADRATA* (Fabricius, 1787)

Ocypode quadrata (Fabricius, 1787), the ghost or sand crab, was initially described in 1787 as *Cancer quadratus* Fabricus. Prior to its current designation, it was also described as *Ocypode albicans* Bosc, 1802.

Members of this genus are distributed in various habitats worldwide but *O. quadrata* is found only along the eastern coast of the Americas from Block Island, Rhode Island, in the northern hemisphere to Santa Catarina, Brazil, in the south (Rathbun, 1918).

The most terrestrial of the decapod crustaceans living along the Atlantic coast of North America, ghost crabs are found in abundance along bordering sand beaches from the mid-Atlantic to the Gulf of Mexico.

Both sexes have chelipeds of approximately equal size which are used to gather/capture prey and for ritualistic territorial displays. Carapace colors range from gray through salt-and-pepper, grayish white, pale yellow to yellowish white, usually approximating the color of beach sand upon which they are found. Yellow markings are found on the legs and lower sections of adult crabs; the young are mottled gray and brown. Cowles (1908), however, reported that ghost crabs responded to light intensity and temperature by changing color.

Mating and spawning seasons for this species vary with latitude, since they appear to be correlated with temperatures. Coues (1871) reported crabs spawn in the Carolinas from April to July. This agrees with the time frame reported for New Jersey (Milne and Milne, 1946) and the Tortugas, Florida (Cowles, 1908). However, Haley (1972) stated that in Texas the crabs were only inactive for a period of about three months when the temperature was below 16°C. With only this short inactive period, ghost crabs found along the Texas coast were able to copulate throughout most of the year, although there appeared to be peaks in spring and summer (Haley, 1972).

Copulation burrows are not essential to successful mating of _O. quadrata_. Hughes (1973) reported that mated pairs were occasionally dug from burrows in Costa Rica. Males in Texas reached sexual maturity at approximately a 24 mm carapace width, females reached the same state at a carapace width of about 26 mm (Haley, 1969).

Egg-carrying females exhibit different behavior than males and females not carrying eggs, by wading and entering the water more freely. During these trips into the water they run along the bottom, and at intervals during times when the water is quiet, they flip onto their backs, open the abdomen and allow water to flow through the egg mass. This insures a good supply of oxygen rich water is available to the developing eggs (Milne and Milne 1946).

Diaz and Costlow (1972) collected eggs from gravid females captured at night. Hatching and development through five zoeal stages were observed in vitro. They usually hatched shortly after they were placed in containers of seawater. Megalopae appeared in a minimum of 34 days. Mortality was high, with less than 10% of all larvae reared reaching the megalopal stage.

Scheltema (1975) stated that: "Among most coastal and estuarine benthic species, gene-flow is largely limited to the dispersal that occurs during pelagic larval development".****"However, gene-flow, even with extensive dispersal, is only successfully completed if immigrants survive to reproduce." Scheltema was discussing benthic species. But, his comments also appear to be applicable to O. quadrata also. Following the release of the zoea into the ocean, ghost crab larvae become a part of the vast planktonic population, subject to long-shore currents and their corresponding counter-currents. The five zoeal stages remain a part of the planktonic assemblage for a minimum of 34 days, after which the megalopae appear (Diaz and Costlow, 1972). During this time, larval dispersion depends on coastal circulation and behavior, particularly vertical movement. No information is available which describes larval behavioral reactions to light, salinity or currents. However, Grant (1979) reported that megalopae of O. quadrata were taken only in surface (neuston) tows of a survey of Mid-Atlantic Bight zooplankton during summer of 1977. Since this survey involved both surface and subsurface (double oblique tows, surface-bottom-surface) collections over 24 hour periods, one could conclude that at least the megalopa stage of O. quadrata is confined or attracted to the surface layer. However, what mechanism or mechanisms initiated or produced this pattern of megalopae dispersal is unknown.

Specific information on the larval behavior of O. quadrata is lacking, but there are reports about other crustaceans in the literature. Milikin and Williams (1984), in their discussion of the blue crab, Callinectes sapidus Rathbun, reported that early zoeal stages were found in surface waters of high salinity (>20 0/00), and were planktonic and positively phototrophic. As zoea mature, later stages were found progressively further offshore. The highest frequency of megalopae were found beyond 64 km from shore and common in surface samples at night. They stated that factors affecting vertical distribution of zoeae and megalopae include light intensity, swimming rate, sinking rate and barokinetic and geotactic behavior. Geotactic behavior was found to vary between zoeal stages with negative geotaxis occurring in stage I and positive geotaxis in stage IV zoeae. They also found that the average duration of the megalopa stage increased with increasing salinity.

Jones et al (1970) reported that the mysis and protozoeal stages of the pink shrimp, Penaeus duorarum Burkenroad, were distributed on the Tortugas Shelf off the coast of Florida mainly between the 8 and 30 fathom contours. Postlarval forms were found both on the shelf and in shallow water. Older postlarval forms were found only in the shallower inshore zone. They stated that water currents were important in larvae movement from offshore spawning grounds to the estuarine nursery zone. Tidal flow may play a role in this inshore movement with larvae riding the flood and clinging to the bottom during ebb tide. They also reported differences in vertical distribution of larval forms by age, with younger larvae found most often near the bottom; and by time of day, with the largest number of larvae found in surface and midwater samples at night.

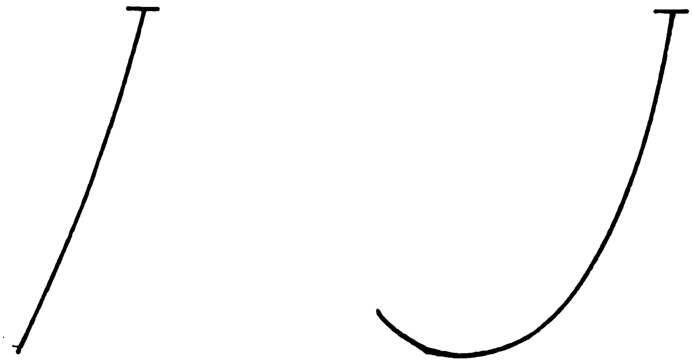
The behavioral adaptations described above do not comprise an exhaustive study of available literature. They do, however, represent examples of mechanisms that could be utilized by O. quadrata to ensure larval form dispersal to habitats where existing populations can be maintained or new colonizations can occur. Additional discussion of this subject will be presented later.

Bumpus (1973) described the oceanic circulation patterns on the continental shelf off the east coast of the United States. He maintained that in spring there is a southward surface current from Cape Cod to Cape Hatteras and a northward surface current from Florida to Cape Hatteras. The Florida to Cape Hatteras current reverses in late summer, when there is a strong southward current from Cape Cod to Florida. However, in certain years when runoff from the Hudson River and Delaware Bay is low, August surface currents north of Cape Hatteras may move northward to Cape Cod. Thus, direction of oceanic currents at spawning time can ultimately make a significant difference in ghost crab distribution.

Northward movement of surface waters from Cape Hatteras to Cape Cod could account for the occurrence of megalopae of _O. quadrata_ found by S.I. Smith in late August of 1870 at Fire Island Beach, Long Island, New York. Smith (1873a, 1873b) further stated that in 1870 no specimens of _O. quadrata_ were found on Fire Island until late August, but that they were common on the outer beach by middle September. However, Smith made a careful search along this beach for several miles and failed to find a single specimen of either an adult or juvenile crab. Smith speculated that all the individuals he had seen, had landed during the current season and that all those from the year before had perished during winter. It is also possible that larval forms of _O. quadrata_ were carried offshore where they were moved north by the Gulf Stream. This theory was postulated by Milne & Milne (1946).

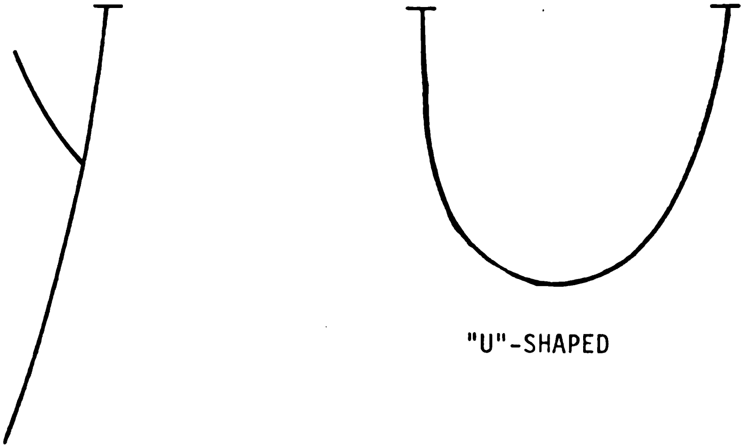
When megalopae develop into the first stage crab and move ashore, conspicuous zonation is displayed in burrow locations of various ghost crab size classes (Williams, 1984). Young crabs, particularly those in the first crab stage, approximately 5-7.0 mm in size, are found close to the high water mark, while those of older and larger crabs are found further from water. Younger crabs usually burrow close to water in a short vertical fashion, whereas larger crabs display more variation in positioning and construction of burrows. Burrows of the latter group normally face the water and slope away from the water at about a 45° angle. They may be straight or have a "J" shaped branch almost reaching the surface. This branch could be used as an escape mechanism when crabs are pursued down their burrow. In addition, burrows resembling a "U" have also been reported (Figure 1). Hill and Hunter (1973) stated that ghost crab burrows showed variable forms in different latitudes. Hayasaka (1935) compared the "sandstone pipes" common in some tertiary sandstones of Formosa to plaster casts made of the burrows of _O. ceratophithalma_ Pallas and found them to be similar. Fisher and Tevesz (1979), Wolcott (1978), McLachlan (1980) and Trott & Robertson (1984) reported that burrow diameter and carapace width were closely correlated with carapace width approximately equal to burrow diameter.

Burrow construction and/or maintenance is conducted primarily during daylight hours (Williams 1984). Following cessation of feeding, about dawn, crabs move inland in search of old burrows or to construct a new burrow. Young crabs usually construct new burrows near water while larger, older crabs burrow further inland usually renovating an existing burrow (Hill and Hunter 1973). Excavated



SLANTED STRAIGHT

"J"-SHAPED



"U"-SHAPED

"Y"-SHAPED

Figure 1 Typical burrow shapes of Ocypoda quadrata burrow sand is brought to the surface by using the walking legs on one side. Sand is either left in a pile at the mouth of the burrow or cast in a fan-like fashion radiating outward. Moist sand is used to plug burrows as the day progresses and temperatures increase. These plugs may remain in place until the crabs re-emerge and begin to forage again during early evening. Some crabs may construct burrows near a large food source such as a beached fish. Burrows constructed close to large objects such as wooden planks are not uncommon.

Early literature (Cowles, 1908 and Phillips, 1940) about these crabs stated that they were primarily scavengers, actively feeding on refuse such as small bits of food buried in the sand's surface, and beached fish, or other animal matter along the driftline. However, Wolcott (1978) stated that scavenged material accounted for less than 10% of their food on North Carolina beaches. Live prey consisting of *E. talpoida* and the coquina clam, *Donax variabilis* Say, made up more than 90% of the ghost crab's diet. Estimates of caloric need coupled with densities indicate that ghost crabs would consume most of the population biomass of these two prey species (Wolcott, 1978). Fales (1976) also reported that ghost crabs fed on mole crabs in North Carolina. Letterman (1973), on the basis of laboratory experiments utilizing mole crabs, various insects and other foods, concluded that *O. quadrata* preferred live prey.

Energy transformed by the filter feeding prey (mole crabs and coquina clam) of the ghost crab is passed on to terrestrial vertebrates who feed on both immature and mature crabs (Walcott, 1978). Phillips (1940), Teerling (1970) Alexander (1979) and Vader (1982) reported that *Ocypode* spp. were preyed upon by birds in New

Jersey, Texas, Seychelles and Kenya respectively, while Teerling (1970) stated that ghost crabs were preyed upon by coyotes in Texas, and McLachlan (1980) reported that ghost crabs were fed upon by mongooses in South Africa.

Cowles (1908) stated that ghost crabs went down to the ocean at intervals to moisten their gills. The crabs do not actually enter the water to moisten their gills. They stop short of the waterline, presenting one side to the water, anchoring the legs of the other side in the sand, and wait for a wave to wash over them. They then return to the higher beach. Following each trip, a small amount of water was retained in the branchial chamber (Edney, 1960).

Bliss (1963) stated that ghost crabs can also take up moisture from damp sand through setae at the base of the second and third walking legs. Water is conducted from the setae into the posterior apertures of the branchial chambers. Wolcott (1976) conducted experiments to determine the mechanism involved in water movement through these setal tufts which are usually located closely opposed and enclose the single posterior aperature to each branchial chamber. He found that two steps were required to accomplish this process: 1) water must be collected by a force exceeding the capillary attraction of the soil spaces, and 2) water must be drawn past the cuticular exterior, into contact with an ion- and water-transporting epithelium for absorption. He showed that these setal tufts were capable of collecting water, and further demonstrated that the ghost crab was actually capable of generating negative pressure (a vacuum) within its branchial chambers. This negative pressure was sufficiently high, enabling it to overcome capillary attraction and draw water from the setal tufts through the posterior aperature into the brachial chamber. In a follow-up study comparing the ghost crab and two gecarcinid land crabs, Wolcott (1984) studied the mechanisms involved in taking up interstitial water from soil and their ecological significance. He stated that soil moisture is apparently a normal source of water for the ghost crab; immersion in the sea is not required for survival. Thus, Cowles' (1908) concept as stated earlier appears not to be totally correct. Ghost crabs usually enter water to escape predation, and exit as soon as possible.

The large stalked eyes of the ghost crab are capable of considerable movement and are well protected when withdrawn laterally into grooves under the anterior edge of the carapace. Given the large and prominent nature of its eyes, one would assume that the animals could see exceptionally well. However, experiments by Cowles (1908) and Milne and Milne (1946) have shown that the eyes are sensitive to differences in light intensity and are used to direct the crab toward moving objects which might be sources of food. While the crabs utilize the eyes to aid in the search for food, the actual detection of food is by taste or smell.

The ghost crab and its relatives spend the vast majority of their lives on the beach and are capable of traveling at a great rate of speed for considerable distances. Normally, locomotion is accomplished by utilizing all eight walking legs, especially when foraging for food. They usually travel sideways or obliquely, but are capable of walking forward and sometimes slowly approach food by walking backward. If hotly pursued, they raise the last pair of legs off the sand and run, using only six legs (Milne and Milne, 1946;

Letterman, 1973). Letterman (1973) also reported that O. quadrata would switch the direction of its body 180° while continuing to run in the same direction. This enabled the crab to maintain maximum speed during flight since it used a different set of muscles. Cowles (1908) reported that ghost crabs, when disturbed, exhibited an unusually fine ability to run directly back to their burrow, in a straight line. This feat was accomplished regardless of the foraging route taken prior to disturbance.

Both Letterman (1973) and Schone (1968) described the aufbaum reaction by ghost crabs. In this display, two crabs raised themselves on their legs, faced each other, chelipeds held apart with the tips pointing downward, or downward and forward. Rarely did the crabs make contact during these encounters and, after a time, the confrontation would end with one crab either flattening itself or dropping the food it was carrying and running away with a sideways motion toward its burrow or ocean.

Three sounds are produced by O. quadrata: bubbling, rapping and rasping. These sounds were detected in burrows in early morning, following a night of foraging (Horch and Salmon 1969, Horch and Salmon, 1972). Milne and Milne (1946) also reported that ghost crabs made a bubbling sound by passing water through their mouth parts. They also stated that on a few occasions a startled ghost crab emitted a short, sharp "peep". This peeping sound, which Milne and Milne speculated was produced by the rapid expelling of air from the gill chambers, has not subsequently been reported. Rapping was done by a disturbed animal when it was alone; rasping (stridulation) was observed following the forcing of one crab into the burrow of another;

and bubbling was found to be produced by lone crabs in burrows (Williams 1984). A single organ (Barth's myochordotonal organ) responds to both airborne and substrate-borne sound, but *O. quadrata* is most sensitive to substrate vibration (Williams, 1984).

ENVIRONMENTAL AND HUMAN DISRUPTIONS

A number of authors have published works which discuss human impacts on barrier islands and beach ecosystems (Teerling 1970; Leggett 1975; Leggett & Butler 1975; Florschuts & Williamson 1978; Smith 1978; Britton 1979; Fisher & Tevesz 1979; Steiner & Leatherman 1979 & 1981). Five of these authors specifically discussed ghost crabs. Leggett & Butler (1975); Leggett (1975) and Steiner and Leatherman (1981) extensively discussed recreational (bathing, off-road vehicles) impacts on O. quadrata. The other authors reported the impacts of human activities on the beach ecosystem using the ghost crab as an organism for indicating impact. In each case, human activities were perceived to be detrimental to their populations.

Of studies that directly discussed ghost crabs and recreational impacts on their population densities, only the report authored by Steiner and Leatherman (1981) specifically investigated this relationship on Assateague Island. Their study, was conducted at four sites within the Chincoteague National Wildlife Refuge on the southern end of Assateague Island. In addition to the four fixed sites, ghost crab counts were taken along the entire island (both Maryland and Virginia) within sites located 1.6 km apart along the length of the beach. They concluded that sites impacted by OVR use had low densities of ghost crabs, while the swimming beach had the highest density. The control site had an intermediate density.

Although using different methodologies than Steiner and Leatherman (1981), both Teerling (1970) and Leggett (1975) working respectively on Padre Island, Texas, and Backbay, Virginia, concluded that recreational activity adversely impacted ghost crab densities. In addition, Fisher and Tevesz (1979) in studies of 13 sites from Cape Henry, Virginia to Cape Hatteras, North Carolina, also concluded that ghost crab densities varied, depending on whether a beach was disturbed or undisturbed. They considered a beach disturbed if it was eroding and/or frequented by pedestrian and/or vehicular traffic. Beaches actively accreting and not frequented by pedestrians or vehicular traffic were termed undisturbed. Although there was no significant difference between the numbers of juveniles on either disturbed or undisturbed beaches, there was a significant difference between the number of adults on these same beaches. However, Leber (1981), in a critique of the statistical methods used by Fisher and Tevesz, decided that statistical irregularities made the conclusions drawn unwarranted.

STUDY AREA

The study area on Assateague Island, (Figure 2), is located within the Mid-Atlantic Region off the east coast of the United States. Assateague is one of approximately 300 barrier islands forming a somewhat continuous chain along the east and Gulf coasts.

Barrier islands generally are long narrow land forms of shifting unconsolidated sand, characterized by a dynamic beach zone. This can include: offshore bars, a surf zone, and the beach itself, followed by a dune zone, interior lowlands, and bayside wetlands. They are separated from the mainland by coastal bays, mud and/or sand flats and usually have wetlands fringing their mainland shoreline.

Most geologists agree on two facts concerning modern barrier islands: (1) they are relatively young geologically speaking, and (2) their formation is related to changes in sea level relative to the land. These sea level changes have taken place as a result of continental glaciation. During cooler glacial periods, water is withdrawn from the sea and stored in the glacial ice cap. The last major glacial period (the Wisconsin period) ended about 12,000 years ago. At that time, sea level began to rise and vast amounts of sand began to move along the Atlantic coast. Additional sediments from deltas and terraces near large river mouths were added to the system and transported along the shore by wave action. Once the rapid rise in sea level stabilized about 4,000 years ago, waves, currents and

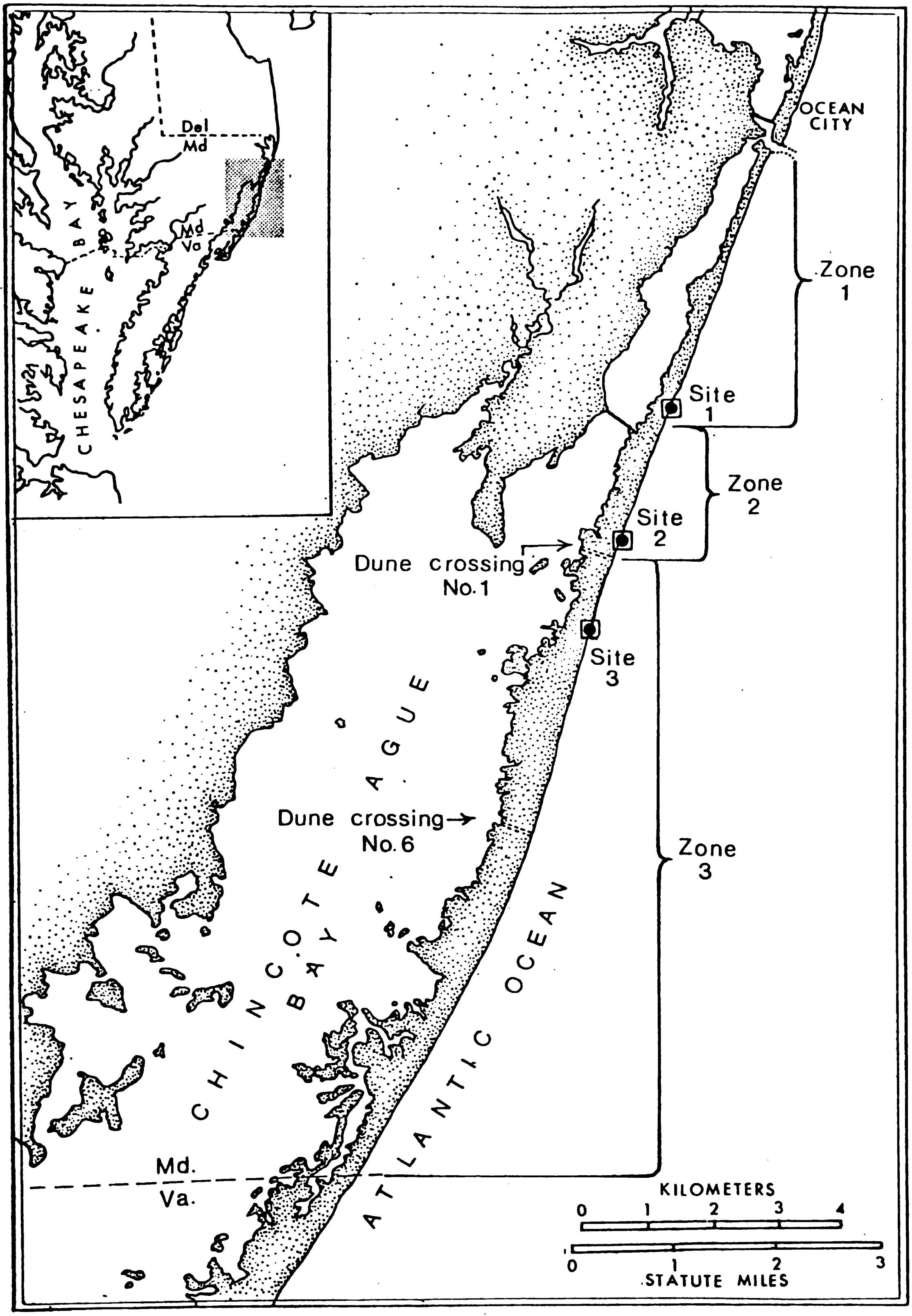


Figure 2 Site location

winds working together on sand surpluses formed the barrier islands of the Atlantic coast. This building process continued for approximately 2,000 years. Since that time, sea level has risen slowly and the barrier islands have been migrating toward the mainland. Today, the coastal processes which formed the barrier islands continue and have resulted in sometimes rapid changes in island configuration (Dolan et al 1977, 1980).

Assateague Island is a typical barrier island 59.5 km in length extending from Ocean City, Maryland, to Chincoteague, Virginia. Wide sandy beaches border the oceanside of the island merging into low, intermittent, frontal dunes backed by a low trough zone. The bayside of the island is bordered by a complex marsh system with numerous sloughs and occasional grassy salt meadow flats. The dunes are sparsely vegetated with salt tolerant grasses and shrubs. Wax myrtle, bayberry and other bushy species form thickets in an irregular zone further back from the beach. Elevations on the island range from 0 to 14.3 m mean sea level, with the highest elevations along the primary dunes and in pine hummocks near the bayside of the island. Mean elevations on the island are 0.9 to 1.5 m above mean sea level. The natural geologic processes of Assateague Island have, however, been altered by man's intervention.

Soils on the island consist of four types of sand (coastal beach sand, kiej and plummer loamy sands, and lakeland sand) and tidal marsh soils which exhibit some clays and have the expected peaty muck texture formed from trapped organic material (Sigrist 1967).

Island climate is strongly influenced by maritime tropical air masses in summer, and by continental polar air masses in winter.

High- and low- pressure systems move from west to east with stable high-pressure systems dominating. Average area annual rainfall is about 119.4 cm with August usually the wettest month. Thunderstorms occur about 32 days/yr, occurring mainly in June, July, and August. Average annual temperature for the area is approximately 13.6°C with the hottest months corresponding to maximum thunderstorm activity. Table 1, (Appendix page 166) lists temperature and precipitation data from three locally available weather stations (Snow Hill and Salisbury, Maryland and Rehoboth Beach, Delaware).

Prevailing winds on Assateague are variable and tend to be within 10° of SE. During summer, the classic diurnal land-seas system of air flow is evident with winds blowing onshore by day and offshore at night.

Wildlife use of the island is extensive including raccoon, red fox, rabbit, muskrat, quail, two species of deer, numerous shore birds and migrating waterfowl, as well as 254 additional species of birds. The peregrine falcon, Ipswich sparrow, eastern pigeon hawk and, occasionally the loggerhead turtle are also found on the island on a seasonal basis (U.S. Department of the Interior, 1982).

MATERIALS AND METHODS

Ghost Crabs:

Three fixed transects were located within the Seashore in areas of differing human use. Transect 1 was located north of the State Park Boundary [the state park boundary forms the border of zones 1 and 2, (Figure 2)] in an area that was subjected to limited human use. This site represented the natural or unimpacted beach and all observations relative to the life history, behavior, etc. of _O. quadrata_ were made at this location. Transect 2 was located across from Ferrylanding Road toward the southern end of zone 2 (Figure 2) and adjacent to the North Beach Campground. This site was chosen to represent an intermediate level of human activity receiving day use, picnicing, and sunbathing from the adjacent campers. Transect 3 was located approximately 1.6 km south of Dune Crossing No. 1 in the section of the seashore that receives off road vehicle (ORV) traffic (Figure 2). This area was picked to represent heavy human use impacts.

At each of the above three sites, a temporary marker consisting of a standard Corps of Engineers survey locator was installed on July 19, 1979. Each marker was surveyed in from a known U.S. Coast and Geodetic Survey (USCGS) or National Ocean Survey (NOS) marker to establish a base line dune elevation. Transect 1 was located utilizing NOS marker H-1-MD-78. A reference point was located 651 m from the marker on a bearing of approximately 37°. The experimental site was located a distance of approximately 113 m from this point on a bearing of 120°. Transect 2 was located utilizing USCGS marker "North Beach No. 2." A reference point was established 64 m from this marker on a bearing of 207°. The experimental site was located a distance of approximately 248 m from this point on a bearing of 120°. Transect 3 was located utilizing NOS marker "P141". The experimental site was established approximately 158 m from this marker on a bearing of 120°. All beach profiles were made utilizing these established markers which were keyed to elevation above mean sea level (MSL).

At each location, density of O. quadrata was estimated utilizing a 3 m square grid along a transect established perpendicular to the ocean from the approximate last high water mark to dune base. The last high water mark was chosen as a reference point since it was always evident. This avoided problems associated with trying to maintain fixed markers and allowed for natural variations in beach width. Initially in 1979 and 1980, this grid was made of string 3 m on a side because all sampling equipment had to be hand carried to the study sites. Following acquisition of a four wheel drive vehicle in 1981, a more accurate 3 m grid was constructed using 2.5 x 5.0 cm lumber which was held together with bolts and wing nuts (Figure 3). This fixed wooden grid was used exclusively beginning with the June 6, 1981 sampling period. In the case of both grid methods, transect location was established by aligning the Corps of Engineers marker on top of the dune with a particular telephone pole along the road. This line was then scuffed into the beach while maintaining the alignment

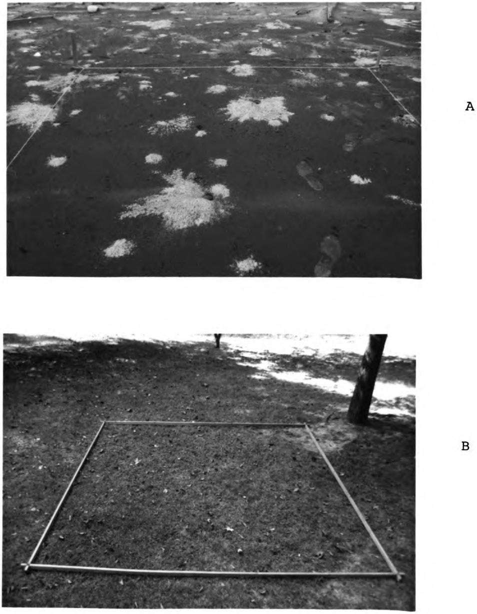


Figure 3 Sampling grids

of the telephone pole and dune top marker. On all sampling dates the grid was placed on the north side of the line. Crab densities were recorded for one location on consecutive days in 1979 and on four occasions at all three transects in 1980 (June, July, August, September).

In 1981 a pair of secondary transects was added to each survey site. These transects were located 20 m to the north (A) and 20 m to the south (B) of the primary transect and were included to allow for a better statistical analysis of differences in ghost crab densities at the three sites. This change increased sample size, and thus reliability, as well as data sensitivity.

Sampling was conducted on a bi-weekly basis on weekends close to full and new moon phases, (Table 2). This allowed investigation of possible differences in activity due to lunar cycle influence. To minimize interference from human activities and to avoid the possibility of blowing sand obscuring burrows, burrow counts were made soon after sunrise. This practice insured maximum accuracy. If blowing sand became a problem during counting, count was terminated and begun anew the following morning.

In 1981 and 1982 for each biweekly sampling period, during the ghost crabs' active period, two transects were surveyed at each sample site. The primary transect was always surveyed and the A & B secondary transects were alternated to avoid biasing the data. The location, diameter and depth of each ghost crab burrow within each 3 m grid was recorded on a survey sheet. The number of burrows within the grid, the average diameter and depth were also recorded. Burrow diameter was measured to the nearest mm and recorded. Measurements

Table 2

Sampling Periods in 1981 and 1982

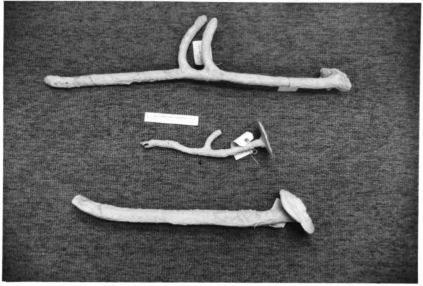
1981		1982	
Date	Moon Phase	Date	Moon Phase
April 17-18	F	April 13	F
May 1-3	N	April 23-24	N
May 15-17	F	May 7-8	F
June 5-7	N	May 21-22	N
June 19-20	F	June 4-6	F
July 3-5	N	June 18-19	N
July 19	F	July 2-3	F
July 31 August 1	N	July 17-18	N
August 14-16	F	August 6-7	F
August 28-29	N	August 20-21	N
September 11-12	F	September 3-4	F
September 25-26	N	September 17-18	N
October 9-10	F	October 1-3	F
October 23-24	N	October 15-16	N
November 5-6	F	October 29	F
November 17	N	November 12	N

were made using a plastic scale placed over the burrow entrance. Measurements were made at the point where the burrow became circular in shape to avoid overestimating the diameter by measuring the cone associated with many burrows. Burrow depths were ascertained by inserting a piece of tygon tubing into all burrows which had a diameter greater than 1 cm. The tubing was withdrawn then measured to the nearest cm and depths recorded. For each day during which a burrow count was taken, the following data were also obtained: air and sea temperature in degrees Fahrenheit (Coast Guard reports temperature in Fahrenheit), wind direction and speed, barometric pressure, an estimate of cloud cover and the times of the high and low tides. The first three items of information were obtained from the U.S. Coast Guard Station located at Ocean City, Maryland. Weather data were transcribed from the 1200 hours entry for the given day. The Coast Guard uses Greenwich Mean Time, thus, their 1200 reading was 0800 hours EST. Cloud cover estimates were made on site and the tidal data were obtained from tables published by the National Oceanic and Atmospheric Administration (U.S. Department of Commerce, 1980 and 1981). All supporting climatic data were converted to metric units.

Casts of crab burrows were made during the first phase of the study and compared to the various types and shapes described in the literature. These casts were initially made by using pure plaster of paris mixed to a soupy consistency so that it could be poured down burrows. Although this technique worked, casts made in this way were weak and all of them broke during excavation. Various materials which could be used to reinforce the castings, such as string, straws or other fibers were considered but discarded because of poor pouring characteristics. Ultimately, a mixture of plaster of paris and quicksetting patching cement was developed which produced a more durable casting. This was mixed using 4.5 kgs of patching cement and 11.73 kgs of plaster of paris. Because of the quicksetting nature of the cement, even with a wet mixture, burrows had to be filled quickly to avoid mixture setting up before it could be poured. Burrow casting was conducted only in the undisturbed area (Transect 1). To allow sufficient drying time casts were poured in the morning and dug the following day. Some casts were dug sooner, but were not completely dried. Casting of burrows was discontinued in 1981 when it was ascertained that burrow types were similar to those previously described in the literature (Figure 4) and because vandals destroyed most castings before they could be recovered.

Various methods were tried or considered for the capture of ghost crabs in sufficient numbers to conduct a mark and recapture study, as well as to investigate migratory patterns. It was also necessary to capture individual crabs as they emerged from their burrows so that carapace measurements could be compared with burrow diameter.

The individual trap technique was originally employed to serve both functions. However, the traps used (typical small mammal box trap, and the small size Hav-A-Hart), both of which were fitted with enclosures to fit over a crab burrow, proved to be ineffective (Figure 5A). A pit trap made from a five gallon plastic bucket was also tried at the same time. This trap was installed on the beach in the evening and removed the following morning. The bucket was partially filled with sand and buried so that its rim was even with or slightly below the sand level. This type of trap was utilized alone, with bait



A

B

Figure 4 Typical burrow casts made on Assateague Island, Maryland.

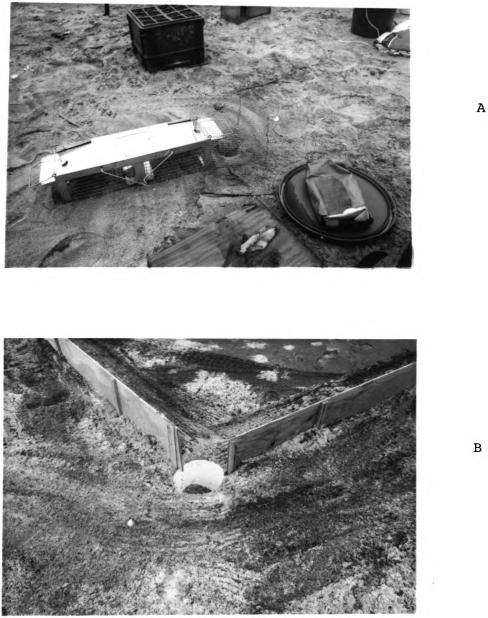
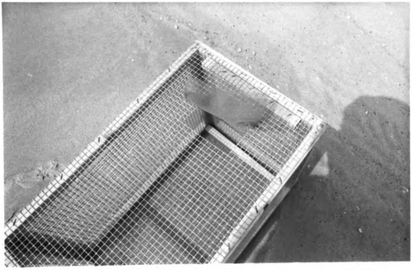


Figure 5 Various types of traps utilized during the study

C



D

Figure 5 (cont'd.)

Figure 5 (cont'd.)

(squid) and without, and in combination with deflector boards made of plywood. Figure 5B and 5C represent a configuration that was utilized. Deflector boards were employed in an attempt to take advantage of _O. quadrata's_ habit of migrating along the beach as they fed. Although the pit trap did catch some ghost crabs, it too was ineffective, catching only a few crabs during each deployment.

Apparently it was not practical to use one trapping method to capture crabs for these aspects of the study. A box trap (Figure 5D and 5E) was ultimately fabricated to catch individual crabs for burrow size evaluation. The trap consisted of a light wooden frame (1.9 cm^2) to which hardware cloth was attached. The top was constructed with a removable panel and the bottom had a section (9.1 cm by 9.9 cm) removed from the center adjacent to one end. This square was covered, in trapdoor fashion, with a section of flexible fiberglass window screen which was stapled to the wooden cross member. The overall dimensions of the trap were: 46.7 cm long, 26.7 cm wide and 34.3 cm high. Prior to the placement of the trap, the diameter of the crab burrow was measured to the nearest mm. The trap was then placed over a crab burrow so that the trapdoor was directly over the burrow and twisted slightly from side to side to bury the bottom under the sand. As the crab exited its burrow, the fiberglass screen would raise up allowing the crab to enter. Once the crab had fully exited the burrow, the screen would fall back into place blocking the hole. The crab could then be removed, marked and measured.

The problem of catching crabs in larger numbers to assess migratory behavior by mark and recapture was solved by taking advantage of a phenomenon observed during routine night-time observation. Crabs remain immobile when transfixed in the beam of a high power flashlight. Milne and Milne (1946) also reported that at night, crabs did not react to humans or approaching lights. Thus, it was possible, on dark nights, to capture numbers of ghost crabs by spotlighting them and physically picking them up by hand. This practice was carried out concurrently with the use of cages described previously, allowing several tasks of the study to be accomplished simultaneously. Crabs captured in individual traps, as well as those caught by hand, were measured using a dial reading vernier caliper. Measurement of carapace width (side-side), length (anterior-posterior) and depth (dorsal-ventral) recorded to the nearest 0.01 mm, sex recorded and the crab marked with red nail polish. Some crabs were coded with a two part number in india ink. This number consisted of the month and the number of the capture, i.e., 4-8 would be the eighth crab captured in April. To ensure that marking did not affect the crabs, several specimens were brought back to the laboratory in Oxford, Md. These crabs were marked and placed in pint jars partially filled with beach sand, and topped with hardware cloth fitted inside the Mason jar ring. The crabs were kept at room temperature, fed rolled oats and the sand was kept damp with sea water. The crabs were captured and marked on 8/27/79 with the first death recorded 21 days later on 9/17/79. Crabs marked and kept in this manner remained alive into late October. The nail polish and india ink numbers were still clearly visable on all dead or alive crabs. Mark and recapture work was only conducted at transect 1.

After marking, visual observations were made on following days in an attempt to locate these crabs. Sections of beach both to the north and south of the release site at transect 1 were observed using binoculars. Observations were made for approximtely 0.8 km on either side of the release site during the day, as crabs were involved in burrow maintenance.

Observations of crab behavior including burrow construction/maintenance, feeding, and agonistic interactions were conducted on a daily basis during each of the 32 sampling trips. An average of 4 observations were conducted on each day of sampling, making a total of 232 individual observation periods. Although observations were conducted at all 3 transects, emphasis was placed on transect 1, the control. This was done to provide observations of ghost crab behavior in an undisturbed setting.

Observations were made at various times of day (morning, noon, evening and night) using binoculars [illegible]mitted. Observations at night were made with the aid of a flashlight. All observations were made while remaining stationary (sitting or standing) on the beach. Several minutes were allowed for crab activity to normalize following disturbance before observations were recorded. Notes were recorded on tape for transcribing at a later date.

Mole Crabs:

Counts of mole crabs were made at each transect location beginning in 1981. Mole crab populations migrate up and down the beach face with the tide. Samples were taken inside (on the ocean side) the current tide line. These counts were made using a three part nesting box sieve (Figure 6). The first box was 42 cm long by 23.3 cm wide by 14 cm deep with a hardware cloth screen measuring

Figure 6 Mole crab nesting box sieve

1.2 cm^2. This box retained the large mole crabs. The second box was 46.3 cm long by 28 cm wide by 14 cm deep with hardware cloth screen measuring 0.8 cm^2. This box held the medium sized mole crabs. The final box, which stood on legs, measured 50.5 x 31.2 x 14 cm with hardware cloth screen measuring 0.5 cm^2. This box captured the small size mole crabs. The box sieve was placed on the beach and sand was shoveled into the top box until it was heaping full (Figure 6A). Water was then splashed over the box to sift out the sand, leaving the mole crabs. These were counted and recorded as small, medium and large. Based on measuring 100 individuals of each size category, i.e. small, medium and large, the mean size of each group (length x width) was: small 14.6 mm x 7.4 mm, medium 18.9 mm x 10.3 mm, large 29.2 mm x 16.3 mm (the data in Table 3, Appendix Page 167). Measurements of mole crabs (to the nearest mm) were made using a dial reading vernier caliper, as follows: length, along the midline from the rostrum to the posterior edge of the carapace; width, at the midline of the carapace. Three replicates were taken at each location. The number recorded for each size group were totalled and averaged to give a single figure for each transect location. The occurrence of coquina clams, amphipods or worms in the samples was also recorded.

Physical And Support Data:

Beach profiles were taken at the previously described locations on July 19, 1979, and again on August 14 and December 8, 1981. The final profile was surveyed on May 11, 1982.

Sand samples were also taken at the same time that the beach profiles were obtained. The numbered points in Figure 7 denote the locations at which an elevational survey was made and a sand sample

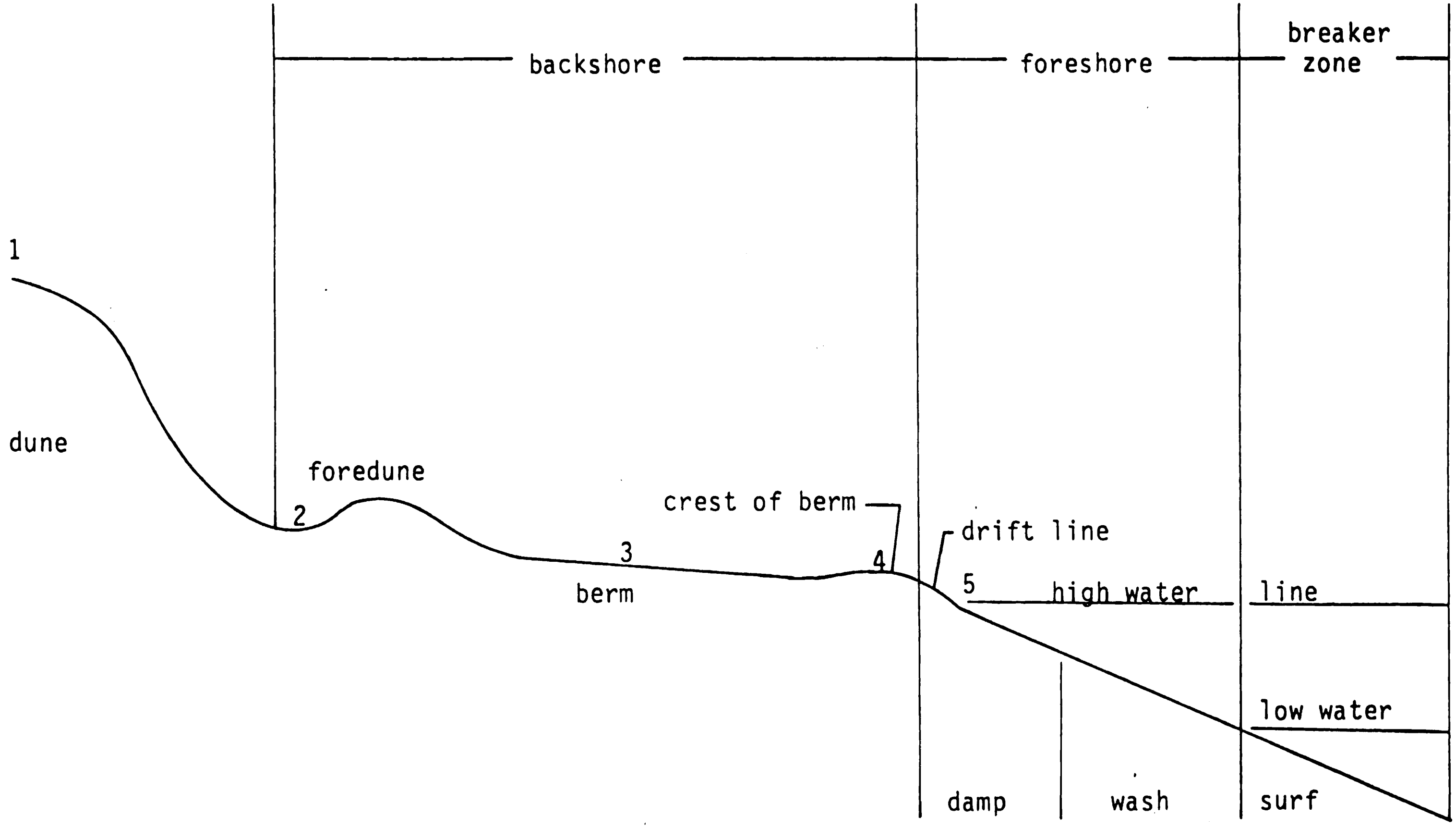


Figure 7 Typical mid-Atlantic beach zonation

was taken. Sand samples were obtained by pushing a plastic pipe coreing device into the sand and removing the volume of sand inside. The device measured 7.6 cm in diameter and was 15.2 cm deep. Approximately 880 cc of sand was taken in each sample. The sand was then placed in plastic bags containing labels noting the date, location, and position on the beach, and taken to the laboratory for later analysis.

Samples were analyzed using a Rapid Sediment Analyzer (RSA) following the methodology described by Byrne, Hobbs & Carron (1982). In this process, a measured sub-sample was placed in the RSA which produces a strip chart depicting proportion of sediment fallen versus time since introduction of the sample to the system. Data were then computer converted to phi-class and recorded as the summed percentage of the entire sample.

In addition to temperature information obtained from the Coast Guard Station, data were also obtained from standard indoor/outdoor thermometers installed on the beach. These units were installed at transect 1 on April 13, 1982. The thermometers were calibrated for both centigrade and fahrenheit scales. One thermometer was installed with its probe located under the beach surface. The second thermometer was installed with its probe located under the beach surface at the end of a section of PVC pipe. This unit was designed to simulate a crab burrow. Both probes were placed approximately 122 cm below the surface of the beach (this depth was chosen to simulate the deepest burrows).

Initially, the thermometers were installed on 9.5 cm^2 supports without protection from the sun. When the afternoon sun struck the units, it elevated the above ground reading. To solve this problem, a box was constructed of white pine measuring 60.3 cm long by 18.7 cm wide by 18.7 cm deep. A door, 24.8 cm long was installed on the front of the box. Aluminum vents were installed and the bottom of the boxes were left open to provide ventilation (Figure 8).

The temperature units were installed so that they would also serve as locators for alternate transects A & B at transect 1. Markers locating the A & B transects were also installed at transects 2 and 3.

ORV surveys to estimate intensity of this type of beach use were conducted during each sampling period. They were generally made between 10:00 a.m. and 2:00 p.m. from Dune Crossing No. 1 to the Virginia/Maryland state line, a distance of about 22.5 km. The survey was conducted by driving a 4-wheel drive truck south along the beach recording the number of vehicles on the beach and the number of individuals engaged in certain activities. Records were kept on the number of individuals fishing, swimming and walking. Individuals engaged in activities not specifically mentioned were listed as "other". The survey was divided into two sections to show differential use of the beach. Traveling south from the entry point, Section I was from Dune Crossing No. 1 to Dune Crossing No. 6, a distance of about 9.7 km. Section II continued from this point 12.8 km to the state line.

In addition, periodic counts of the number of ORVs entering and exiting the oversand (that area of the National Seashore open to ORV's) area were also made. These counts were taken near the entrance

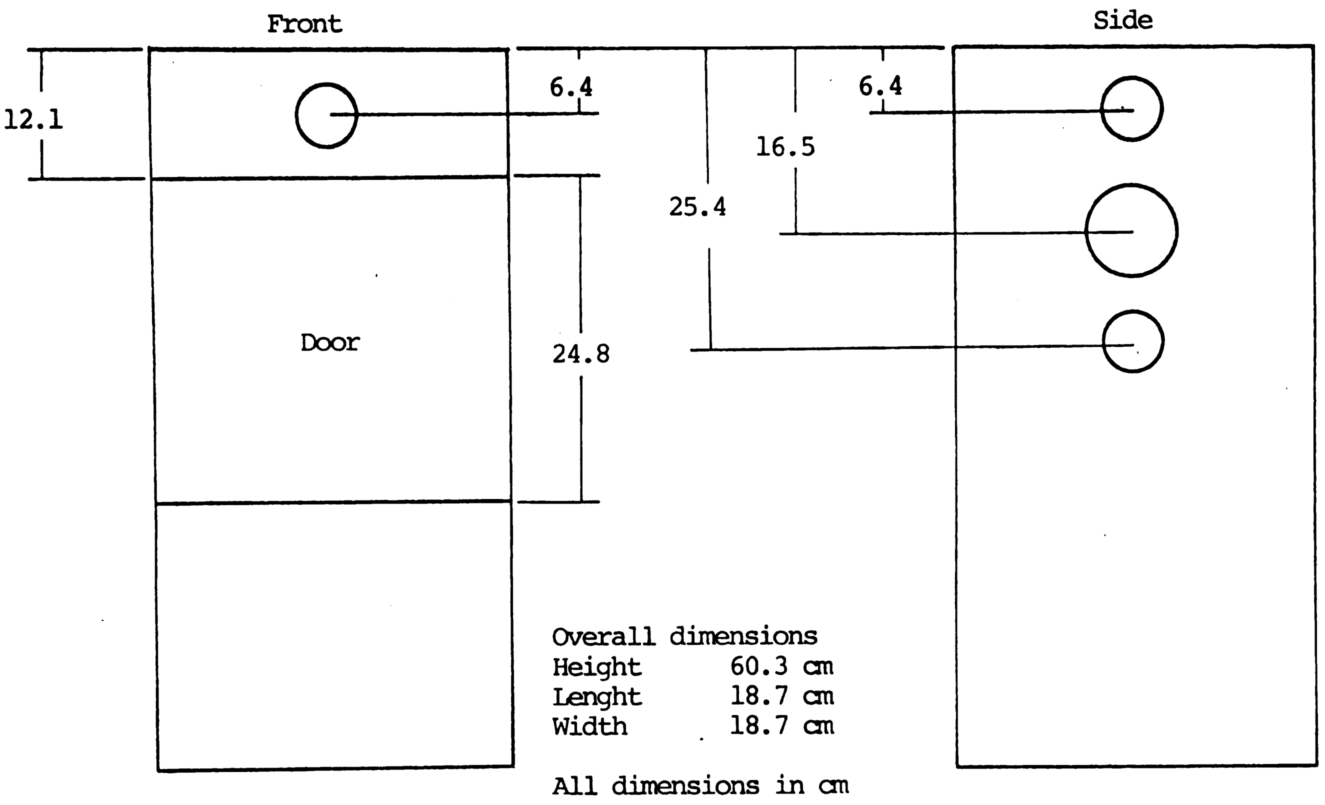


Figure 8 Thermometer shield with vents

to the oversand area. Counts were taken for a measured time period so that they could be related to an hourly or daily rate.

Surveys were also made of the intensity of human use in the North Beach day use area in front of transect 2. These surveys were conducted at three separate beach locations. The first was located in front of the main North Beach parking lot area; the second was at transect 2; and the third was located in front of the North Beach south parking lot at the end of the paved road. At each of these sites, the number of individuals engaged in swimming, fishing, walking, and sunbathing was recorded. As in the ORV survey, all individuals who were not specifically engaged in one of these activities, were noted as "other". All individuals within approximately 50.0 m to the north and south of a central location at each site were included in the count.

The time of day that these surveys were conducted would have an influence on the results. This was especially true in the area adjacent to transect 2 where campers would most likely leave the beach at lunch time and return to their camp sites. Weather also played an important role in intensity of human use. For these reasons, every effort was made to standardize the time periods during which these data were collected. However, since collection of ghost crab data was paramount, it was not always possible to keep an exact schedule. As a result, the times of the day that these surveys were conducted, varied from sampling period to sampling period, as well as within sampling periods.

Statistical Analysis:

Data gathered relative to ghost crab density, burrow diameter and burrow depth were analyzed utilizing the student "t" test to determine if the mean values were statistically different. The values compared were the mean values calculated utilizing the data from both the primary and secondary transects.

Size class distributions of ghost crab populations at transects 1 and 2 were evaluated using the Kolmogorow-Smirnov Two Sample Test (Sokal & Rohlf, 1981). No statistical evalution of data gathered at Transect 3 was conducted because of the small sample size.

Mole crab populations at all three locations were compared using Friedman's method for randomized blocks (Sokal & Rohlf, 1981). In this case, the various sample dates represented blocks and the three locations, treatments.

A ratio similar to that described by Fisher and Tevesz (1979) was developed to evalute recruitment. Instead of the adult-to-juvenile ratio used by Fisher and Tevesz, a ratio of the sum of size classes No. 2-5 (1.6 - >4.5) to size class No. 1 was used to investigate recruitment. All new recruits fall into size class No. 1, thus, this ratio should be sensitive to size changes of this group.

When the ratio equals 1.0, there were equal numbers of juveniles and adults. When the ratio was less than 1.0, there were more juveniles than adults and when the ratio exceeds 1.0, there were more adults than juveniles. When this ratio was displayed graphically, all lines showing a positive slope indicated an increase in number of adults and lines with a negative slope indicated an increase in number of juveniles.

No statistical treatment was used for the beach profiles, sand grain analysis or various measurements of human use.

RESULTS AND DISCUSSION

Physical

Sand Grain Analysis:

Analysis of the sand samples provided a mean phi class value for each sample with an associated standard deviation. Table 4 (Appendix page 168) shows these data. The smallest value recorded was 1.04 phi while the largest was 1.93. Table 5 (Appendix page 169) displays the relationship between phi class, grain size (mm) and sediment type. Using the range of phi values given above, all the values fell into the medium sand classification with a grain size of 0.25 to 0.42 mm.

Figure 9 represents these data graphically. The similarity of each transect's grain size was apparent when the graphs were overlaid. Even the graphs of grain size from the various sample dates were similar when compared in this fashion. Station 5 showed the greatest fluctuation. This was expected since this station was located in the active surf zone where sediments were continuously being deposited, washed and graded.

All locations when compared on the same sample date or between sample dates had very similar grain sizes. Therefore, sand grain size was not a factor which influenced ghost crab ecology.

Beach Profiles:

The beach profiles at all three locations showed similar and expected seasonal trends. Each location increased in height and width

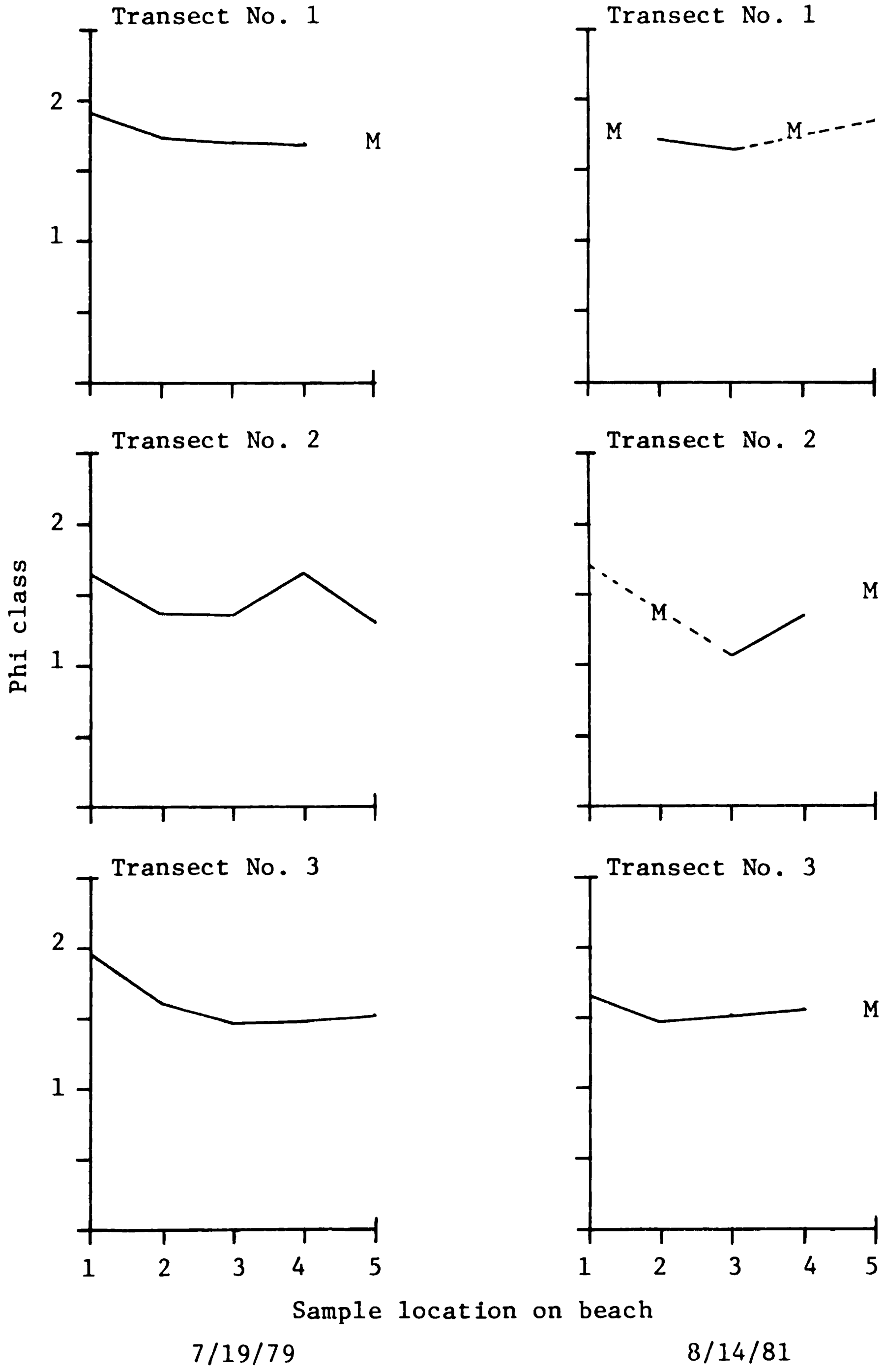


Figure 9 Phi class plotted against beach location by transect for the dates recorded.

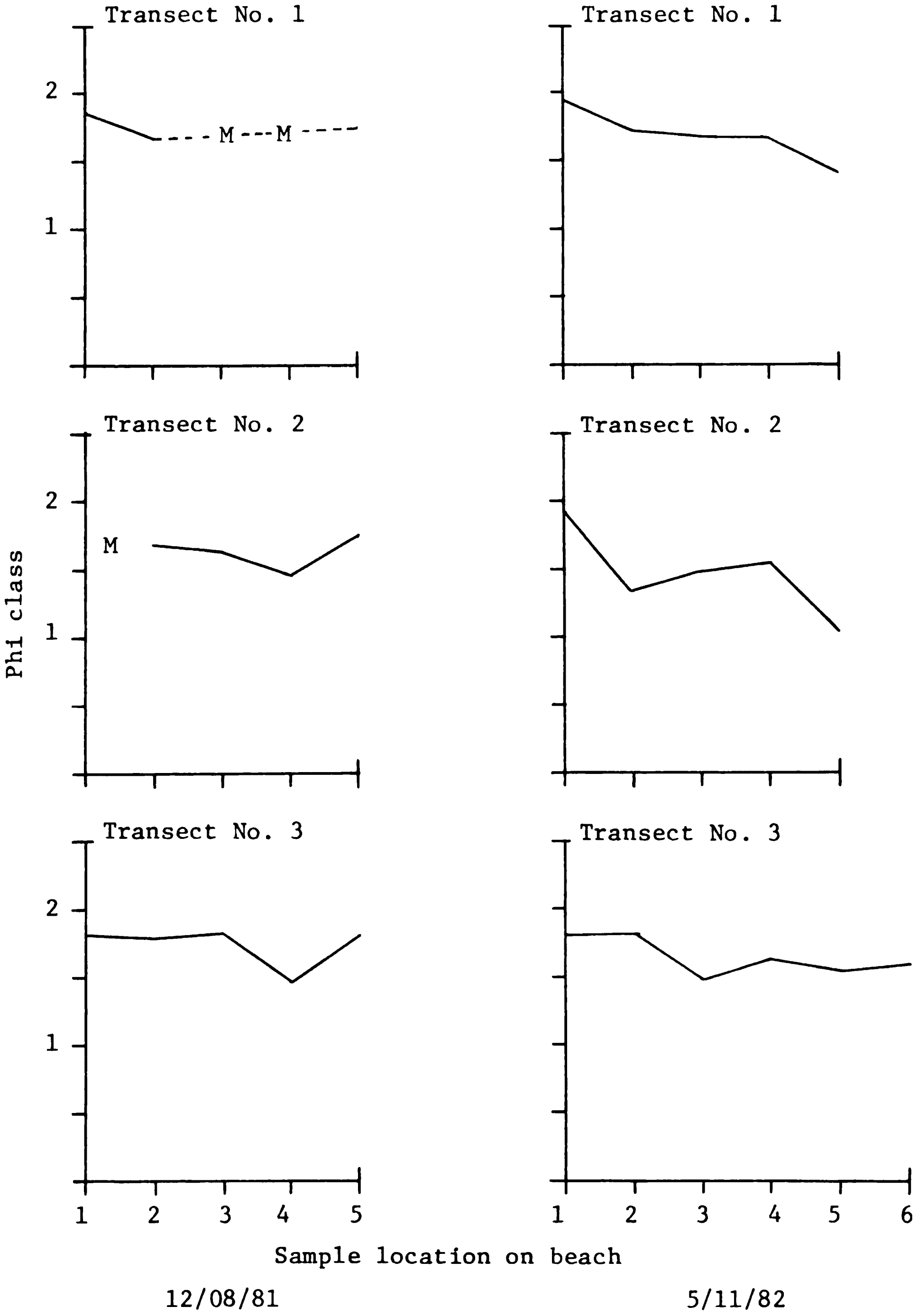


Figure 9 (cont'd.)

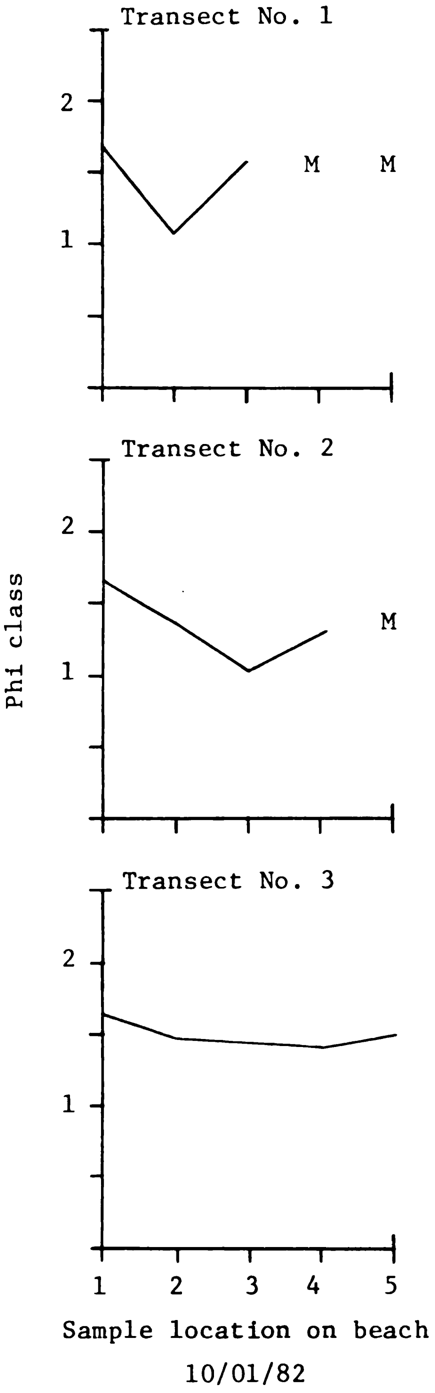


Figure 9 (cont'd.)

over the summer as sand was transferred from offshore bars. Each location steepened in slope and decreased in height over the winter as the sand which had accreted over the summer moved offshore.

The primary difference between locations was beach width. To some extent there was a difference in dune height and shape. At transect 1, the back shore was approximately 36.6 m in width in the summer of 1981, while it was in excess of 76.2 m in width at the other two locations. The height of dunes varied from about 4.6 m at transect 1, to 5.2 m at transect 3, with an intermediate value at transect 2. Only transect 3 showed a small foredune (a smaller dune located in front of the primary dune) of approximately 1.5 m in height.

Figures 10 and 11 depict profiles of study beaches. The beach profiles appeared to be similar. Therefore, the assumption was made that beach topography would not differentially influence ghost crab ecology.

Temperature:

Figures 12-14 show temperature data collected during the two years of study (data in Tables 6-8 Appendix pages 170 & 172). When compared with average air temperature information (Table 1, Appendix page 166) a similar trend was indicated. Temperatures began to rise in March, peaked in July and August and then fell through December. Figure 14 shows surface and undersand temperatures recorded on-site at Transect 1 during 1982. These data show trends similar to data obtained from the Coast Guard at Ocean City, Maryland. However, since these data were not always taken at the same time as Coast Guard data, they cannot be directly compared. In 1981, temperature and wind

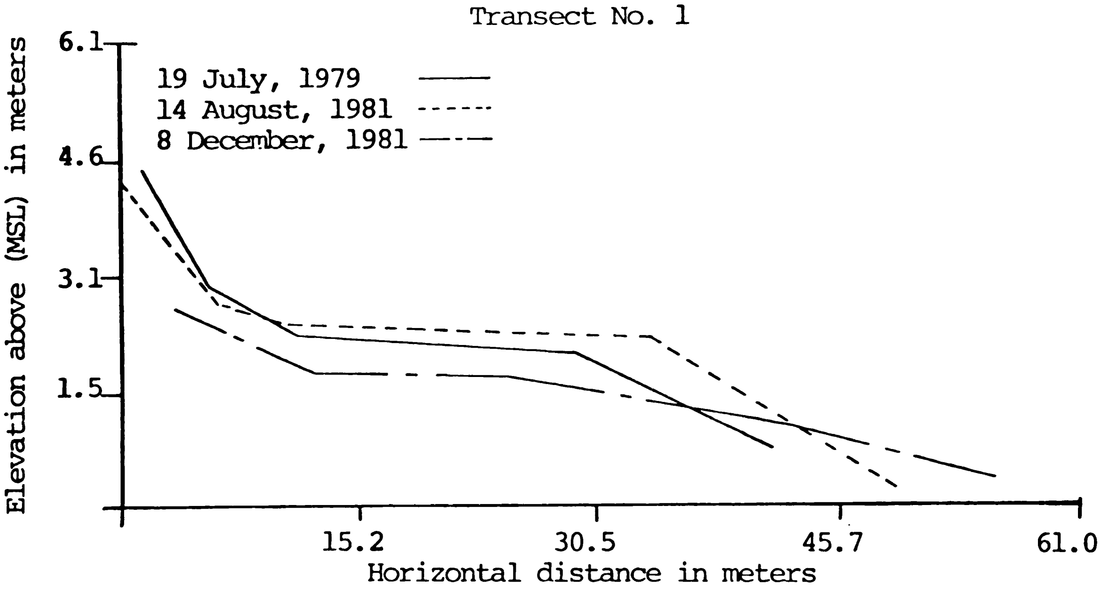


Figure 10 Beach profiles for transect 1 for the dates recorded

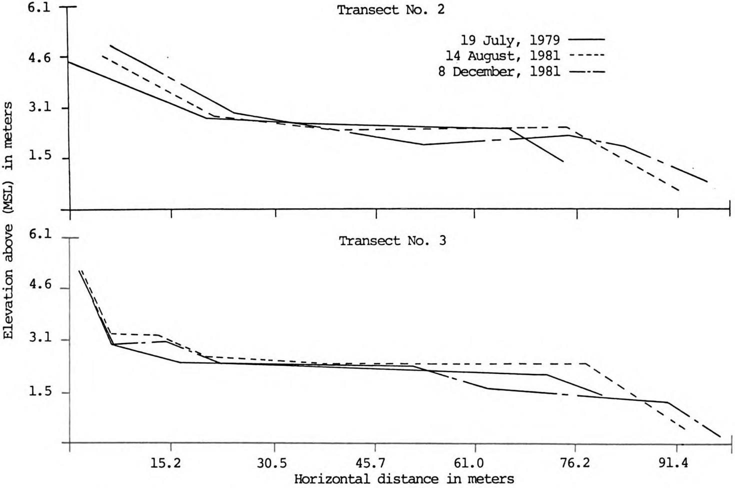


Figure 11 Beach profiles for transect 2 & 3 for the dates recorded

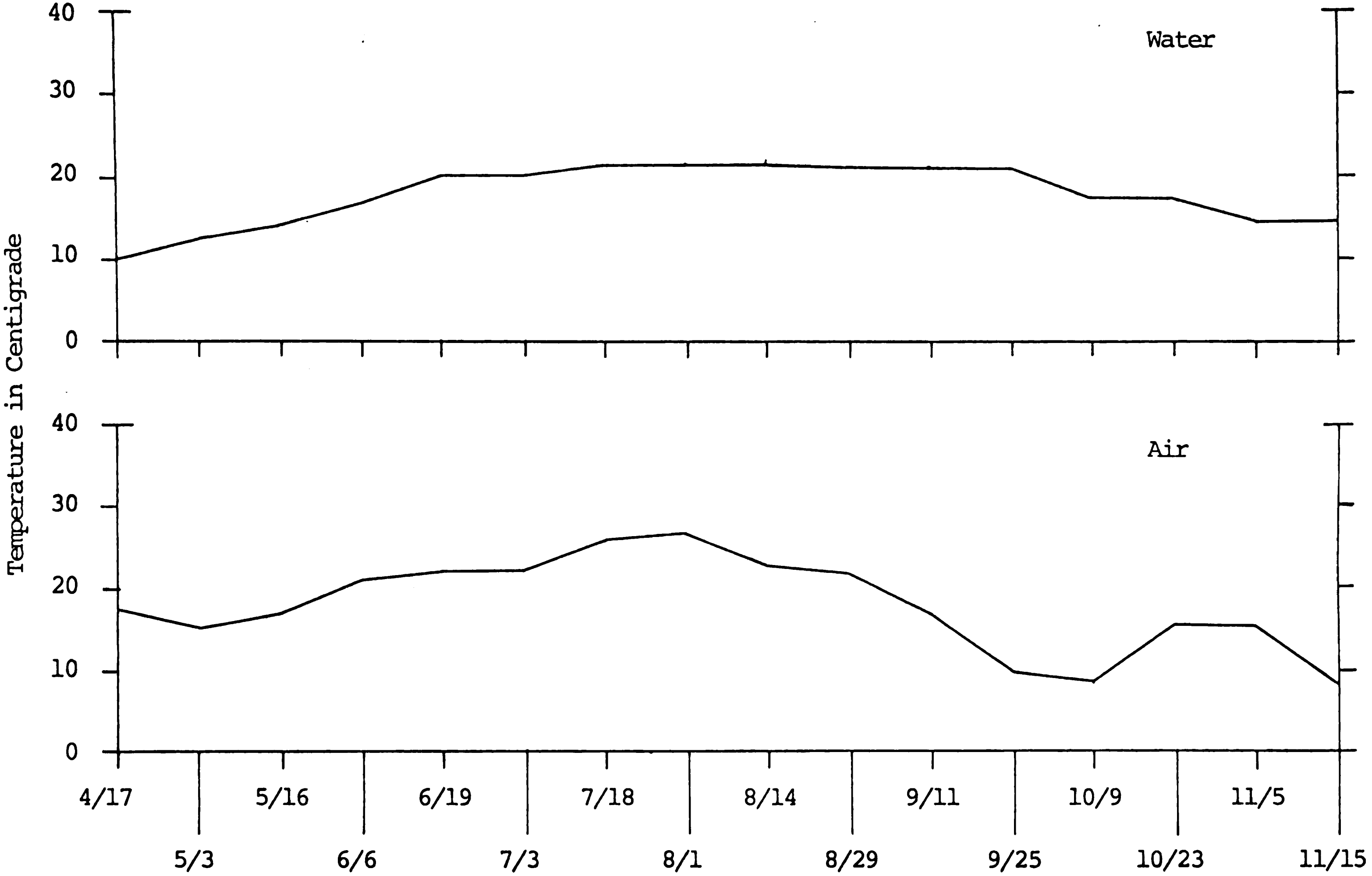


Figure 12 Air and water temperatures from Coast Guard records for the dates recorded in 1981

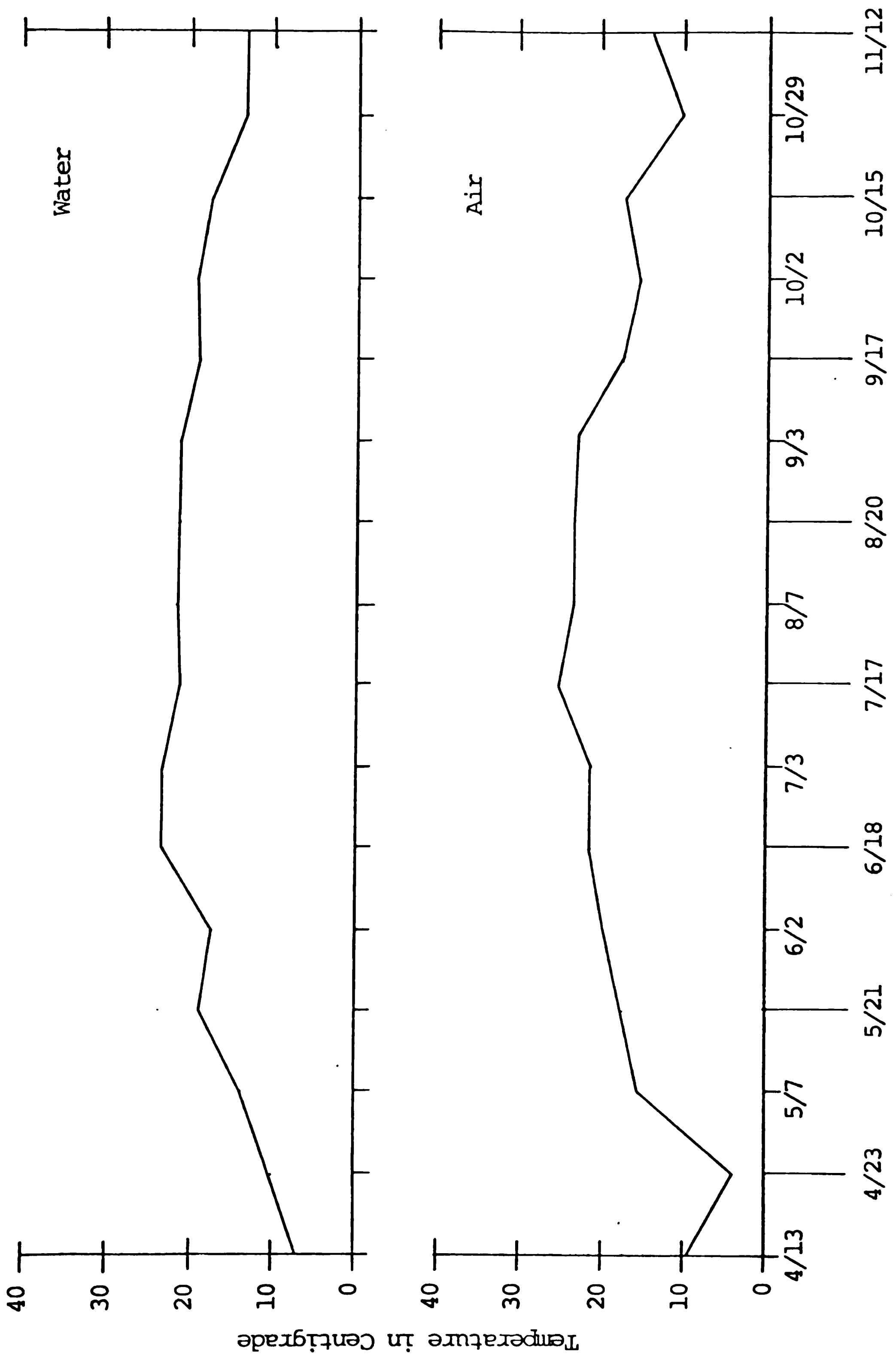


Figure 13 Air and water temperature from Coast Guard records for the dates recorded in 1982

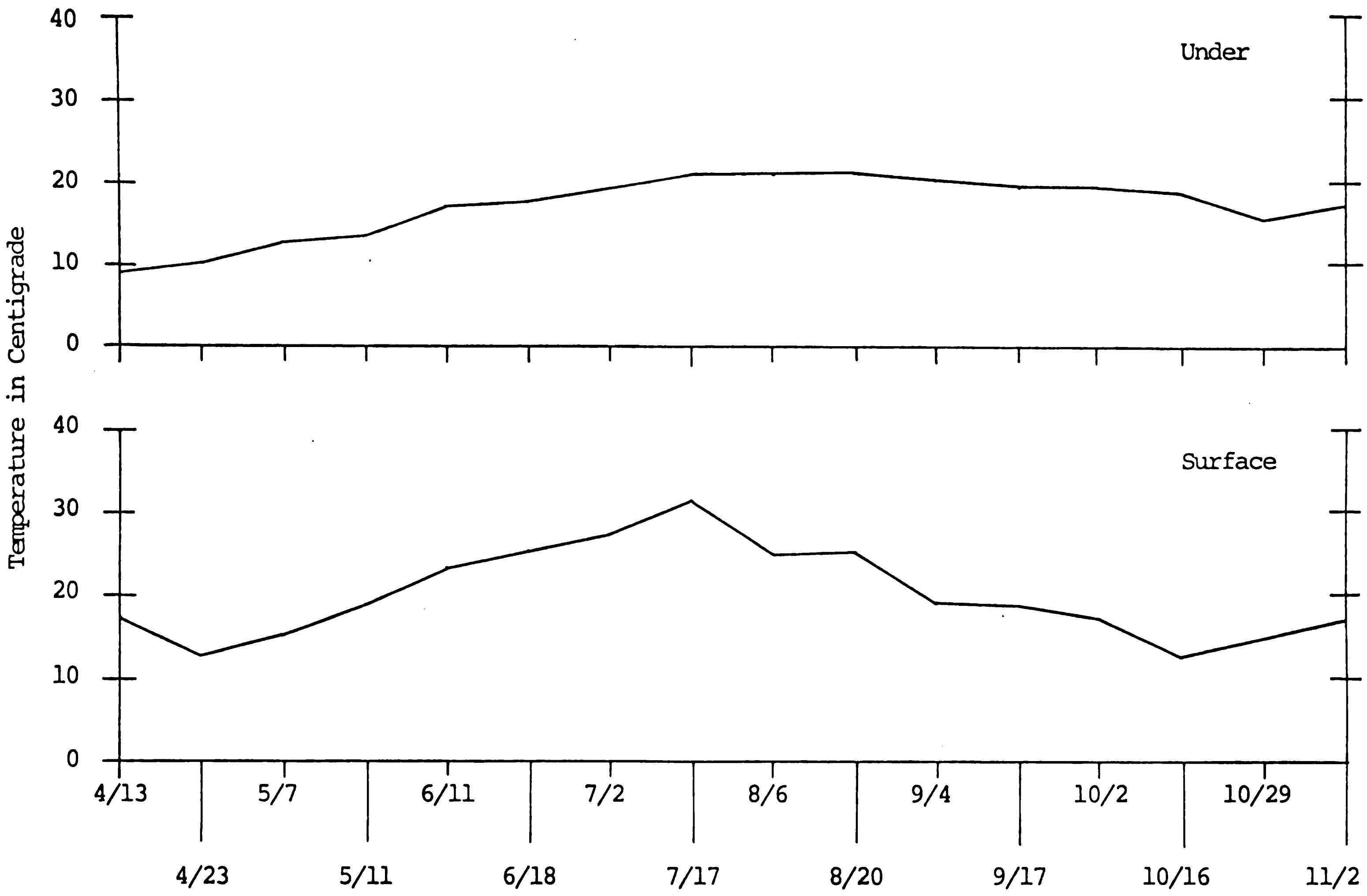


Figure 14 Air and under sand temperatures from transect 1 in 1982

velocity/direction data taken from 4/17 to 11/5 represent actual sample dates. Sample dates for 1982 are 4/13 and 11/12 respectively. Data before and after these dates were obtained from Coast Guard data sheets and are included for informational purposes. Comparing undersand temperatures (Table 8, Appendix page 172) with sea temperatures (Table 7, Appendix, page 171) a similar pattern can be seen. However, undersand temperatures never became as warm in summer or as cold in winter as adjacent ocean water temperatures. In fact, undersand temperatures remained rather stable, varying only 14° from a low of 7.7°C in January of 1983 to a high of 21.7°C in July/August of 1982. This stability and narrow range of temperature fluctuations could be important to ghost crabs since it may affect their ability to overwinter. In addition, it could be related to their emergence in early summer.

Wind Direction/Velocity:

Tables 6-7 (Appendix pages 170 & 171) show wind velocity and direction on selected and sample dates in 1981 and 1982. Figure 15 depicts a wind rose for data gathered at Wallops Island, Virginia for March 1945 through June 1957 . Teerling (1970) reported that there was a relationship between wind velocity, regardless of its direction, and the number of ghost crab burrows. She found that as velocity increased (>10 knots), the number of ghost crab holes was suppressed. She also stated that northerly winds tended to suppress burrow densities. Upon examining maps depicting the location of Teerling's experimental sites on Padre Island, Texas, I observed that north winds tended to blow along the main axis or length of the

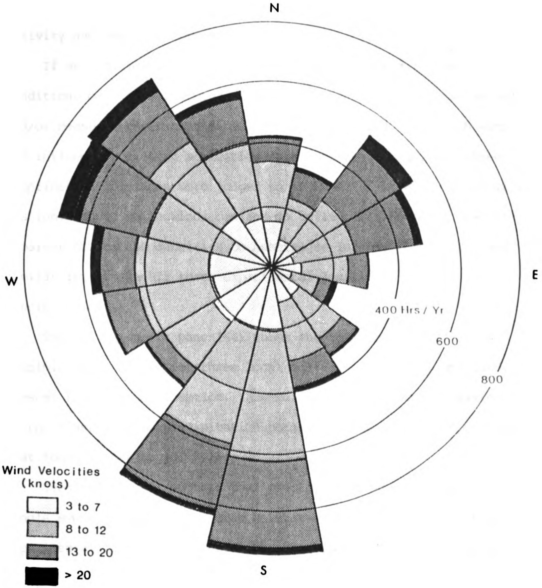


Figure 15 Wind rose for Wallops Island, Virginia, located directly southwest of Chincoteague Inlet. Duration of wind velocities expressed in hours per year averaged from data of National Weather Service, March, 1945 to June, 1957. (From Bartberger, 1973)

island. This most likely resulted in blowing sand which reduced crab activity and obscured burrow entrances.

If an individual experimental site was subjected to these conditions on a more frequent basis than other locations, the actual and/or measured ghost crab densities may be reduced. Although wind did influence burrowing activities on Assateague Island, all three experimental locations were judged to be impacted by wind in a similar fashion. Thus, while winds can and do influence either the real or apparent ghost crab densities on Assateague Island, they would have similar impacts on all three experimental locations.

Precipitation:

Table 1 (Appendix page 166) shows the total monthly precipitation, in cm, for three local cities. Snow Hill, Maryland, is closest to the study location. However, Rehoboth Beach, Delaware, is on the coast and its precipitation pattern should closely approximate that found on Assateague Island.

Teerling (1970) reported that precipitation above 25 mm (for a single event) reduced ghost crab hole densities. Since all three experimental locations are close together and, in general, receive the same amount of precipitation, all three experimental locations would be affected evenly. Therefore, precipitation would not differentially effect ghost crab densities at the three sites.

Human Impacts:

Human impacts on the beach and its associated ecosystem occur as a result of four activity categories: (1) ORV use of approximately 22.5 km of beach from Dune Crossing No. 1 to the Virginia/Maryland line; (2) travel on the beach by official vehicles; (3) campers utilizing the North Beach, Bayside, hike-in and group camping facilities; and (4) day use by visitors.

Tables 9 & 10 (Appendix page 173 & 174) show park usage by various categories by month during 1981 and 1982. Also recorded were dates on which various campgrounds opened and closed. The bulk of park use was during May through August, with a considerable amount through September and October. This May-October period corresponds well with ghost crab activity. In 1981 and 1982 this same time frame accounted for 82% and 87%, respectively, of park use by visitors.

Figure 16 shows the various human uses recorded for the ORV zone in 1981 and 1982. In each case the greatest percentage of individuals were involved in the "other" category, followed by fishing. Swimming and walking, although switching positions between years, were a distant third and fourth. As expected, the percentage of walkers fell from Section 1 to Section 2 because of increased distances traveled. Data from the ORV surveys is contained in Tables 11 and 12 (Appendix, page 175 & 176).

Figure 17 shows the various categories of activities engaged in by park users at three separate locations in 1981 and 1982. In each case, the percentage of individuals engaged in the various categories of activities remained similar between 1981 and 1982, especially at transects 1 and 2. The shift in percentages between 1981 and 1982 at North Beach south parking lot can be explained by the small sample size (n=1) in 1981.

When categories of uses were compared in 1981 and 1982 similarities could be seen between percentages of individuals found walking in the ORV zone (13% & 10%), North Beach south parking lot

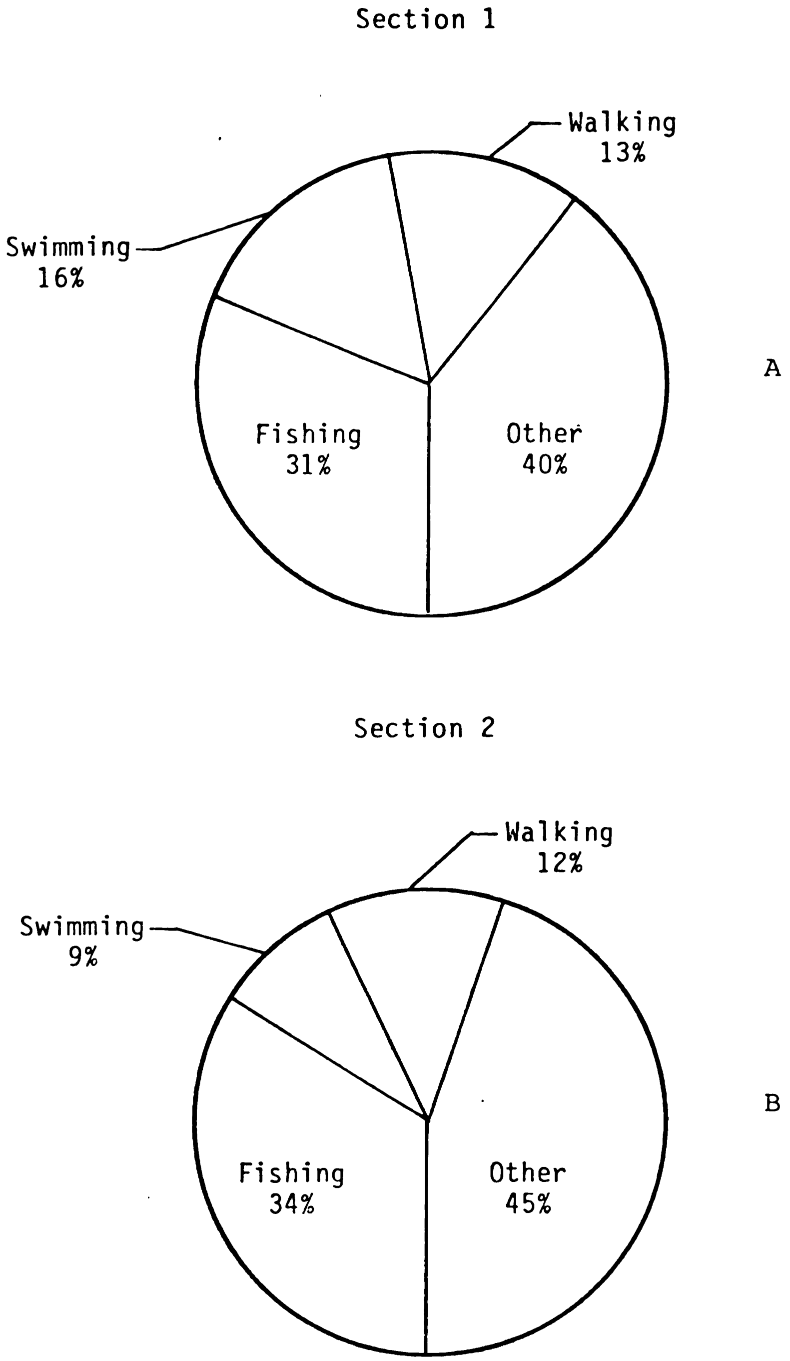
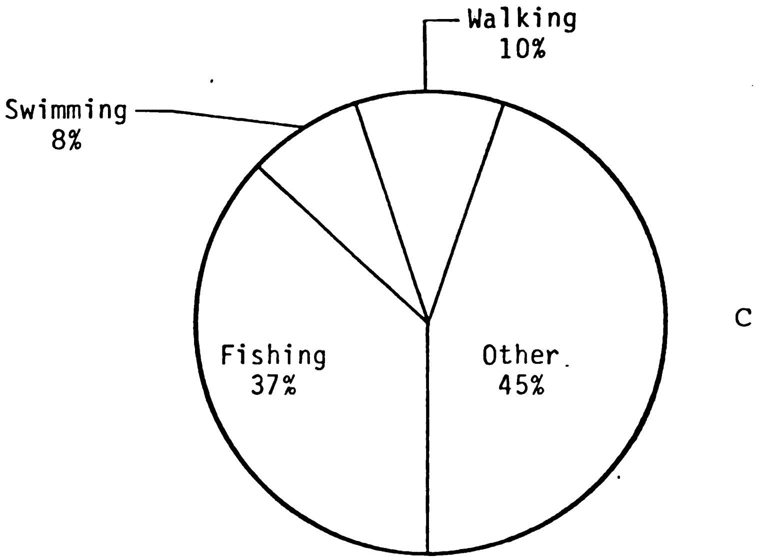


Figure 16 The percentage of individuals involved in various activities in the ORV zone in 1981 (A & B) and 1982 (C & D)

Section 1



Section 2

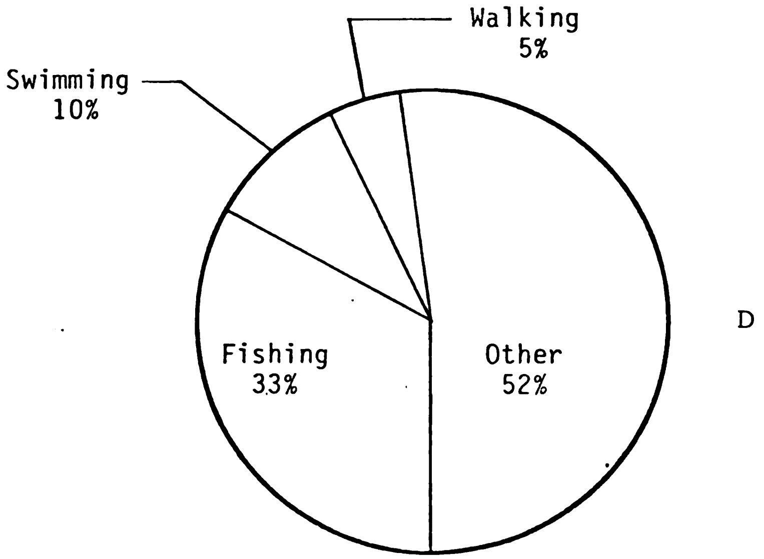
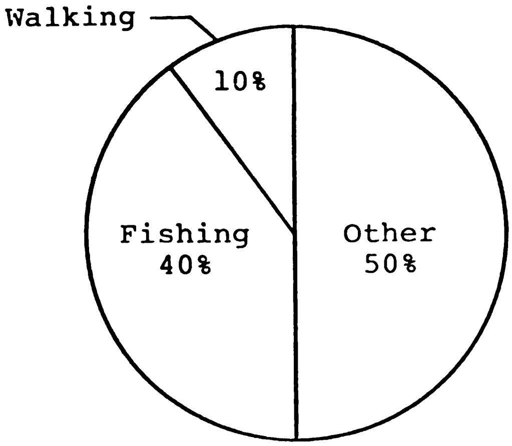
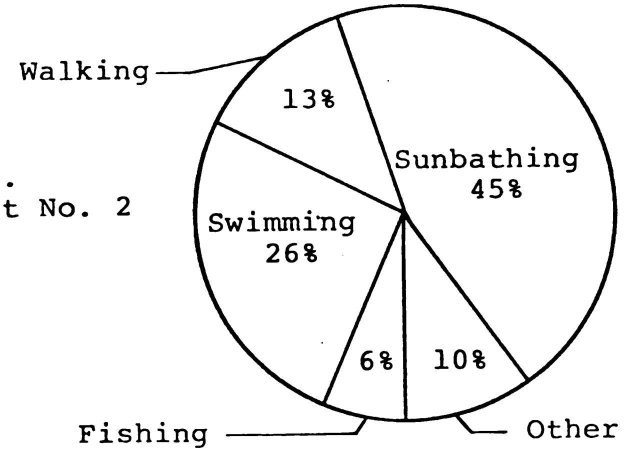


Figure 16 (cont'd.)

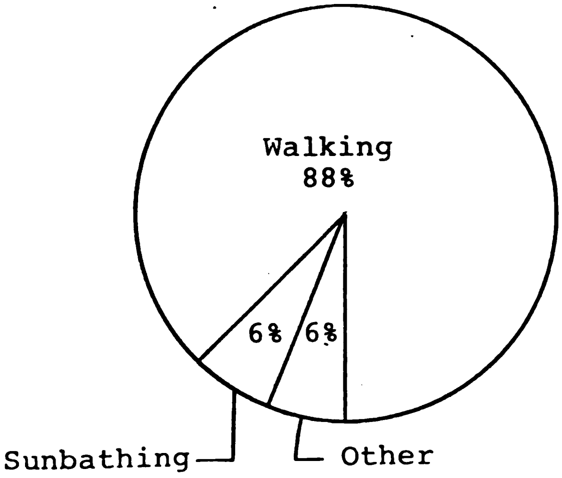
Figure 17 The percentage occurance for each activity for the site reported. 1981 (A, B, & C), 1982 (D, E & F)



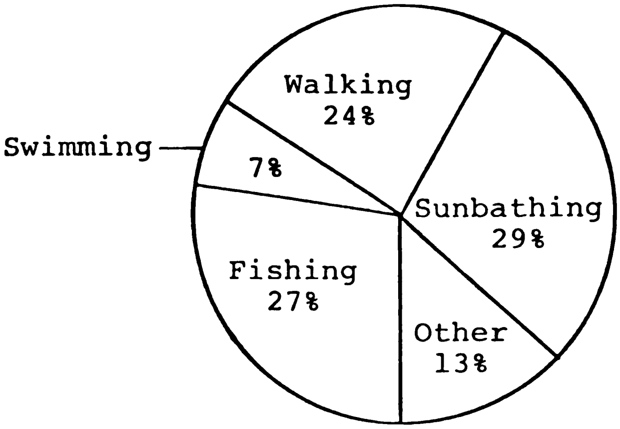
A.
North Beach south
parking lot



B.
Transect No. 2

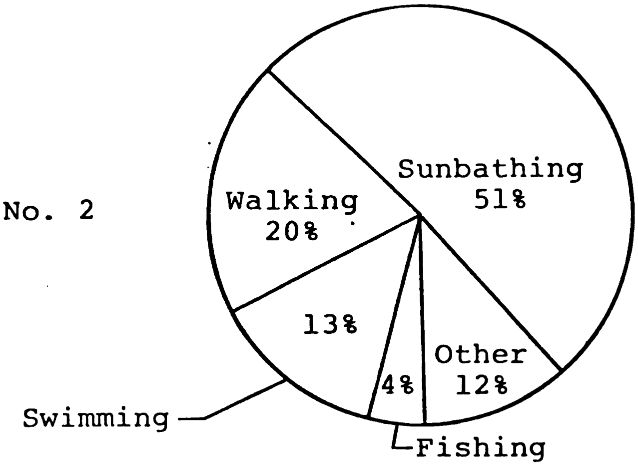


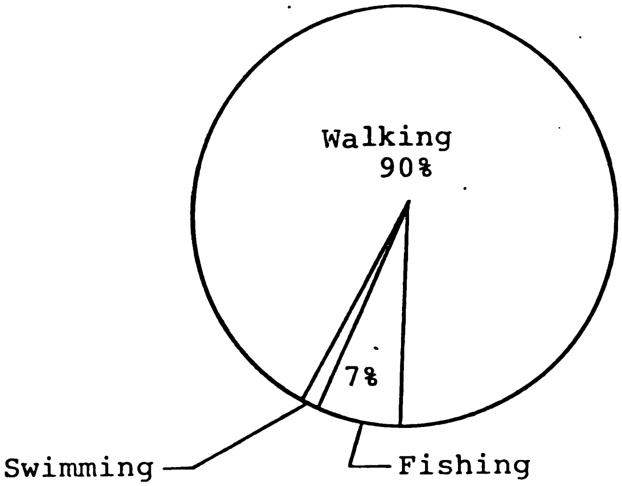
C.
Transect No. 1



D.
North Beach south
parking lot

E.
Transect No. 2





F.
Transect No. 1

(10% & 24%) and transect 2 (13% & 20%). The percentages of individuals involved in the other uses (swimming, fishing, and other) were not comparable, with the exception of fishing at the North Beach south parking lot. This compares favorably with ORV zone figures.

Summary:

Physical factors, i.e., sand grain size, beach slope, temperature and precipitation, in the three study areas were very similar. Therefore, ghost crabs should not select one location over the others as a result of differences in physical characteristics. However, human activities which take place in these three areas were quite different, and may influence the survival, growth and reproduction of the crabs.

Biological

Mole Crab:

Wolcott (1978) reported that the mole crab *E. talpoida* was a primary source of food for *O. quadrata* on Bogue Banks, North Carolina. A study of mole crab relative abundance at all three locations was included to ascertain their availability as a food source for *O. quadrata*, and to determine the influence of human activity on mole crab populations.

The mole crab study was begun on April 17, 1981. On June 5, 1981, the three box sampler was completed. Samples were measured and catagorized as small, medium, or large. Data were collected for the study duration on a biweekly frequency.

For each date in 1981 and 1982 the total number of mole crabs captured at each transect was analyzed using Friedman's Randomized

Block Method. This analysis showed that mole crab populations at all three transects were not significantly different (P=.05). Just why these mole crab populations were not significantly different when they were subjected to different stresses requires some discussion. One would logically expect that ghost crab predation or ORV impact would reduce the abundance of mole crabs. As a result a larger mole crab population would be expected at transect 2 where ORV activity and ghost crab predation was reduced (ghost crab abundance lower at transect 2 than at transect 1).

ORV impacts on mole crab abundance should be minimal since they inhabit the wash zone (Figure 7 page 37) and move up and down the beach with the tide, while ORV traffic normally takes place on the backshore. This traffic pattern results because most ORV operators want to keep their vehicles out of salt water.

If ORV impacts were not affecting mole crab abundance, why did we see no reduction in abundance as a result of ghost crab predation? Several possible hypotheses could explain this: 1) the data gathered were not adequate to detect subtle differences in abundance; 2) recruitment/reproduction of mole crabs was high enough to replace losses due to predation or conversely ghost crab predation was so low that it did not reduce mole crab abundance; or 3) the highly mobile mole crab population continually redistributed itself along the beach, evening out impacts resulting from ghost crab predation.

Figures 18-19 depict the total number of mole crabs by transect and date for 1981 and 1982 (data in Tables 13 and 14, Appendix Pages 178 & 181). In both 1981 and 1982, a peak abundance of mole crabs occurred during August and the first part of September. There was

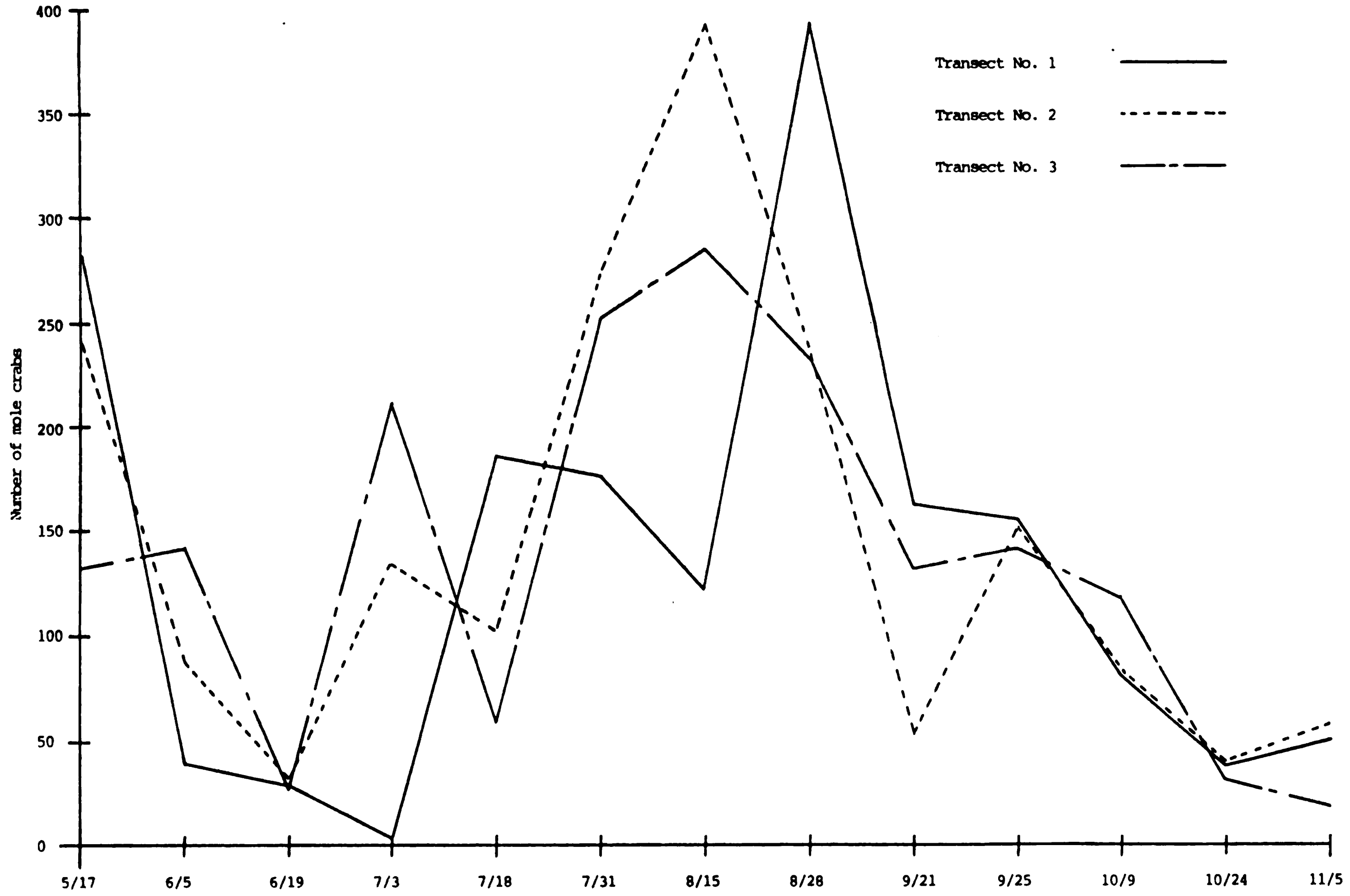


Figure 18 Total number of mole crabs plotted by transect and date for 1981

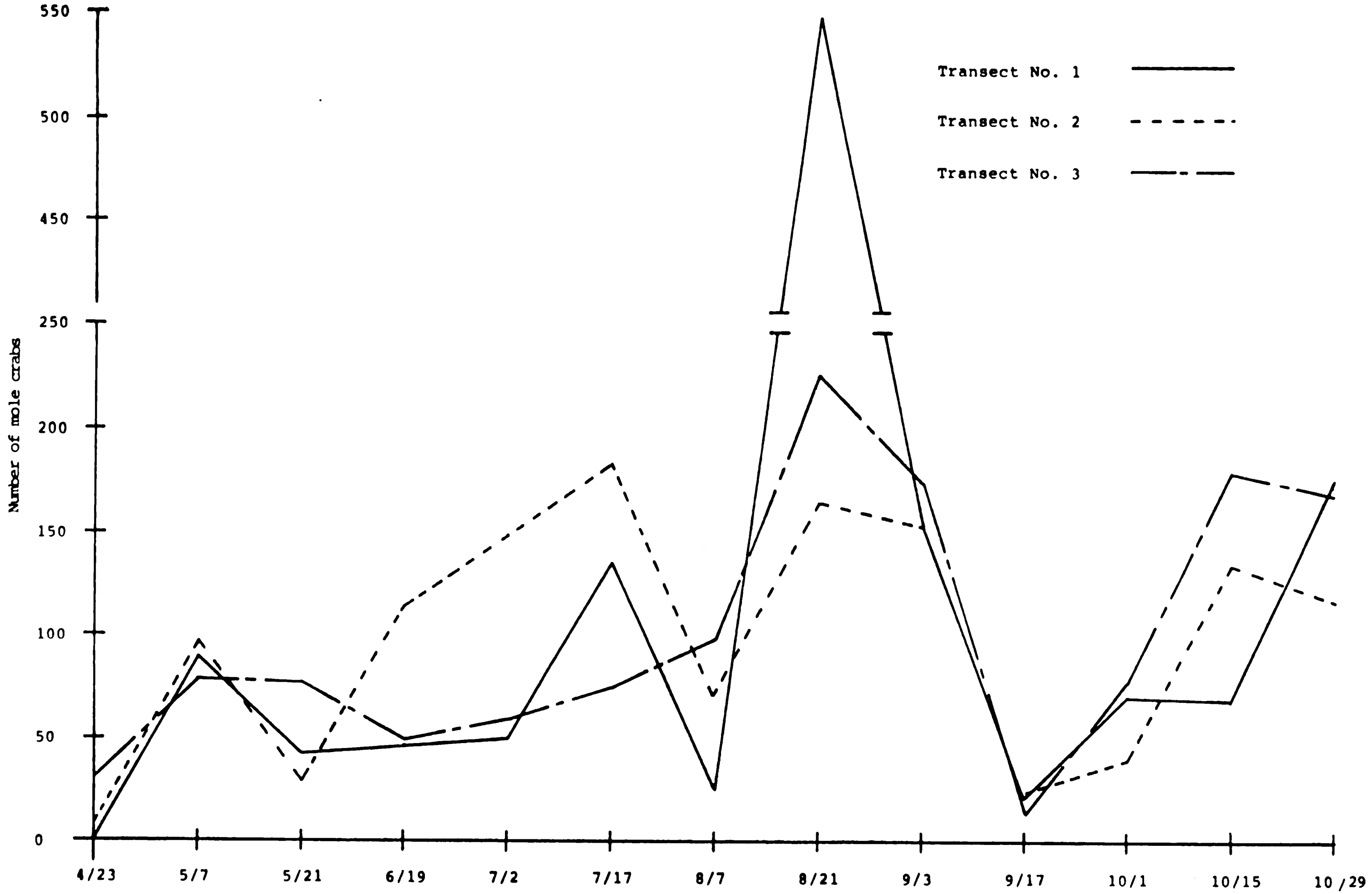


Figure 19 Total number of mole crabs plotted by transect and date for 1982

also a strong secondary peak in October, 1982, although 1981 data show a downward trend during this same period. The 1982 data conform rather well to the recolonization periods of June-July and September-October reported by Diaz (1974) for this species in North Carolina.

Gravid females were collected starting with the first sample in April and continuing through the middle of August, 1981. In 1982, gravid females were first taken May 7th, when orange ova were seen on the ventral surface of their abdomens. During the following sampling period (May 21-22, 1982), brilliant orange egg masses were evident between the telson and ventral surface of the abdomen. The egg masses were not as brilliantly orange colored on individuals collected on July 19, 1981. This information basically conforms with that published by Williams (1984), who stated that the spawning season lasts from winter to autumn. He reported that the spawning season varied in length with latitude, being longer in the south than north. He also stated that as eggs mature, they change from orange to a translucent dirty gray just prior to hatching.

Since mole crabs must face the same problems in larval retention and recruitment as *O. quadrata*, a brief discussion of its larval development and recruitment strategies follows: *E. talpoida* required 28 days, in vitro, to develop from hatching to megalopa through 6 larval stages (Rees, 1959). Hanson (1969), working with *Hippa cubensis* (De Saussure), showed that the relationship between temperature and zoeal development time is linear, with larval development time being extended with decreasing temperature.

Sandifer (1973) stated that in plankton collections most of the records for *E. talpoida* larvae were from along shore or in bays and lagoons close to the ocean. Some records showed evidence of a slight offshore migration. Megalopae and young adults were found to be evenly distributed in the wave-washed zone, while adults there tended to form colonies (Wharton, 1942). E. talpoida, once on the beach, moves back and forth with the tide, following the receding waves toward the water or moving up the beach with the deeper waves. They overwinter offshore in 2 to 4 m of water. In North Carolina, they leave the beach in October and return in January (Diaz, 1974). Although sampling on Assateague Island did not begin early enough to detect the first recolonization, the data showed a definite spring increase, followed by a fall decline. Mole crabs were still present on the beach in November, 1981 and late October, 1982.

Efford (1970) posed four possible mechanisms by which E. analoga (Stimpson) might be recruited to the beaches it inhabits along the Pacific Coast of the Americas: (1) counter current hypothesis; (2) gyral hypothesis; (3) nursery area hypothesis and (4) rearing current hypothesis. He provided evidence for accepting the counter current hypothesis which depends on existence of a current running parallel to the coast and an associated surface or subsurface counter-current. When these conditions coexist, larvae are carried up and down the coast as they drift in side eddies from one current to the other. Thus, unless the current speeds are very different, a great number of larvae tend to remain quite close to the coastline from which they originated. When they drift near shore, those zoeae ready to moult into megalopae would do so, and by staying in the surface water drift passively to the beach with an on-shore water movement. The fact that Sandifer's (1973) review of planktonic records failed to find significant numbers of off-shore records for *E. talpoida* tends to support Efford's hypothesis.

In a follow-up study Efford (1976) discussed the distribution of the nine known species of *Emerita*. He showed that (with the exception of *E. portoricensis* Schmitt, which has an island distribution) this genus was generally limited in its distribution to long coastlines where counter currents exist. If one considers the northerly flowing Gulf Stream and southern flow from Cape Cod to Cape Hatteras described by Bumpus (1973) as the two currents required, Efford's hypothesis could be used to explain distribution and recruitment patterns of *E. talpoida* on the Atlantic coast.

A similar mechanism might be responsible for distribution and recruitment of members of the genus *Ocypode*, particularly if one compares the world-wide distribution of the various members of these two groups. In every location where Efford reported the existence of the genus *Emerita*, there were one or more members of the genus *Ocypode* present.

Ghost Crabs:

Reproduction

Reproduction, or various aspects of it, within the genus *Ocypode* has been discussed in papers by a number of authors (Schone, 1968; Hughes, 1966, 1973; Haley 1969, 1972; Diaz and Costlo, 1972; de L. Brooke, 1981). Other authors have mentioned this aspect of *Ocypode* biology in their papers discussing this cosmopolitan genus (Cowles, 1908; Milne & Milne, 1946; Jones, 1972; Letterman, 1973).

Based on data collected during the 1981/82 field work, *O. quadrata* was reproductively active on the beaches of Assateague Island from June through September. This observation was based on the capture of a gravid female in July 1981, the collection of gravid females during July and August 1982 and the observation of copulating pairs on June 6, 1981, July 17, and September 3, 1982. In all three cases copulation occurred on the beach outside the burrow.

One copulatory event occurring on June 6, 1981, was observed from its inception. It occurred on the beach at transect 1 shortly after sunset (approximately 2115 hours) during a new moon sampling period. Normal crab feeding behavior was being observed when a smaller crab (female) moving south along the beach was noticed. There were several larger crabs attempting to capture mole crabs on the edge of the surf. When the female approached to within 0.5 - 1.0 m of these other crabs, one (male) rushed forward and seized her walking legs in his chela. The female, following a brief period of struggle, remained passive during the remainder of the event. Following the capture, the male manipulated the female using his chela and her walking legs until she was in a nearly vertical position facing him. The male then raised up on his walking legs and slipped the female under his abdomen. The male then rocked back slightly and both crabs were then in an almost vertical position relative to the beach. Close inspection showed that the male had forced open the female's apron and inserted his copulatory organs. At this point, the crabs became disturbed, separated and fled. The time involved up to this point was between 1 1/2 and 2 minutes. This description agrees with that reported by Hughes' (1973) for two instances of copulation in _O. quadrata_ that occurred within a laboratory enclosure. However, Hughes witnessed the entire event which lasted approximately 25 minutes.

Hughes also reported that there was no indication of any enticement or active participation on the part of the female during the entire encounter, which was similar to the observation reported here.

Of the three copulatory events observed during this study, two took place during sampling periods near the time of the new moon (June 6, 1981; July 17, 1982) and one was near full moon (September 3, 1982). All three events occurred during the evening following sunset, and two of the three occurred at or near the water's edge. The two events which took place near the time of the new moon were also associated with high crab activity on the beach, especially near the water. This compares favorably with the findings of de L. Brooke (1981) who noted that on Cousin Island, Seychelles, *O. ceratophthalmus* (= O. ceratophthalma) usually constructed its copulation burrows near the new moon. Letterman (1973), reporting on observations made on Green Island N.Q., Australia, stated that mound building for this species tended to be more frequent near full moon.

Copulation by *O. quadrata* on the open beach has also been observed in May, August and September on the Texas Coast by Haley, (1972), at mid-morning in September on the coast of Costa Rica by Hughes (1973), and at night during low tides near the water's edge on Bogue Banks, North Carolina by Horch (1975). This activity (by *O. occidentalis* Stimpson) was observed at night in August on the Pacific Coast of Costa Rica. In addition, Letterman (1973) reported on observing *O. ceratophthalmus* copulating on an open beach in Australia.

Haley (1972) stated that although he had seen copulation on the beach only in May, August, and September, it probably occurred throughout the year. He suggested that the increasing length of day could be a stimulation for copulation, with the peak activity occurring during the summer months. However, Cowles (1908) reported that in the Tortugas, the breeding season appeared to be in spring and early summer. Based on data collected during this study and considering the difference in climate/activity period, copulatory period on Assateague Island falls well within limits reported for southern populations of *O. quadrata* in the literature. In addition, copulation of *O. quadrata* on Assateague Island appears to be similar to that reported for this species along the Atlantic and Gulf coasts south of Assateague.

No author has specifically investigated the time needed by *O. quadrata* to reach sexual maturity. Haley (1972) hypothesized a time frame using information about other species. He observed that at 23°C *O. laevis* Dana took about 45 days from ovulation to hatching. Costlow and Fagetti (1967) had determined that *Cyclograpus cinereus* Dana needed 46 days (20 days as megalopa) at 20°C from hatching to first crab stage. Using this information, Haley (1972) concluded that the entire developmental period of *O. quadrata* from ovulation to first crab stage should take about 60 days. Since *O. quadrata* are active in Texas from late March until mid-December, he concluded that first crab stages should appear on the beach in July. There was an apparent bimodal period of reproduction in Texas *O. quadrata*, with a second influx of first stage crabs predicted for October. Utilizing the more recent work of Diaz and Costlow (1972), on *O. quadrata* specifically, Haley's estimates of first crab appearance are still within reason, although most likely short.

Building on his earlier work, (Haley, 1969) which used histological and morphological evidence to determine the size of O. quadrata at puberty (males >24 mm, females >26 mm), Haley (1972) calculated the time it should take a first crab female to attain puberty. Starting from a first crab measuring 7.0 mm and using data published by Rao (1968) which showed that under experimental conditions O. cordimana Desmarest exhibited growth increments of 16-20 % per moult, he calculated (assuming a 20 % growth increment) that 7 moults would be required to reach a carapace width of 25 mm. Paulraj, et al (1982) reported male and female O. platytaris (Milne-Edwards) showed distinct signs of maturity at a carapace width of 30 mm. While Crane (1941) stated that O. gaudichaudii Milne-Edwards and Lucas anatomically appeared to reach maturity at a length of around 22 to 24 mm.

Using 7 moults and a moult frequency of 35 days, (assuming no moulting in January and February, the crabs' inactive period in Texas) Haley (1972) concluded that the May and August broods could attain puberty by March and July of the following year. This agreed with an influx of pubertal females he found in both spring and summer. Based on this, and assuming a stable population, he predicted that a female ghost crab might live for almost three years, spending the first year as a juvenile.

June was the beginning of the major reproductive period on Assateague Island. Using Haley's estimate of 60 days from ovulation to first crab stage, first crab stages should appear on Assateague Island in August. This pattern was particularly evident in the size class histograms for 1981 (see Figures 20 & 21). Haley's information has been used to predict when juveniles reaching Assateague Island

Figure 20 Total number of crabs (recorded by burrow count) for each transect reported by size class for each sampling period in 1981

○ Full moon ● New moon

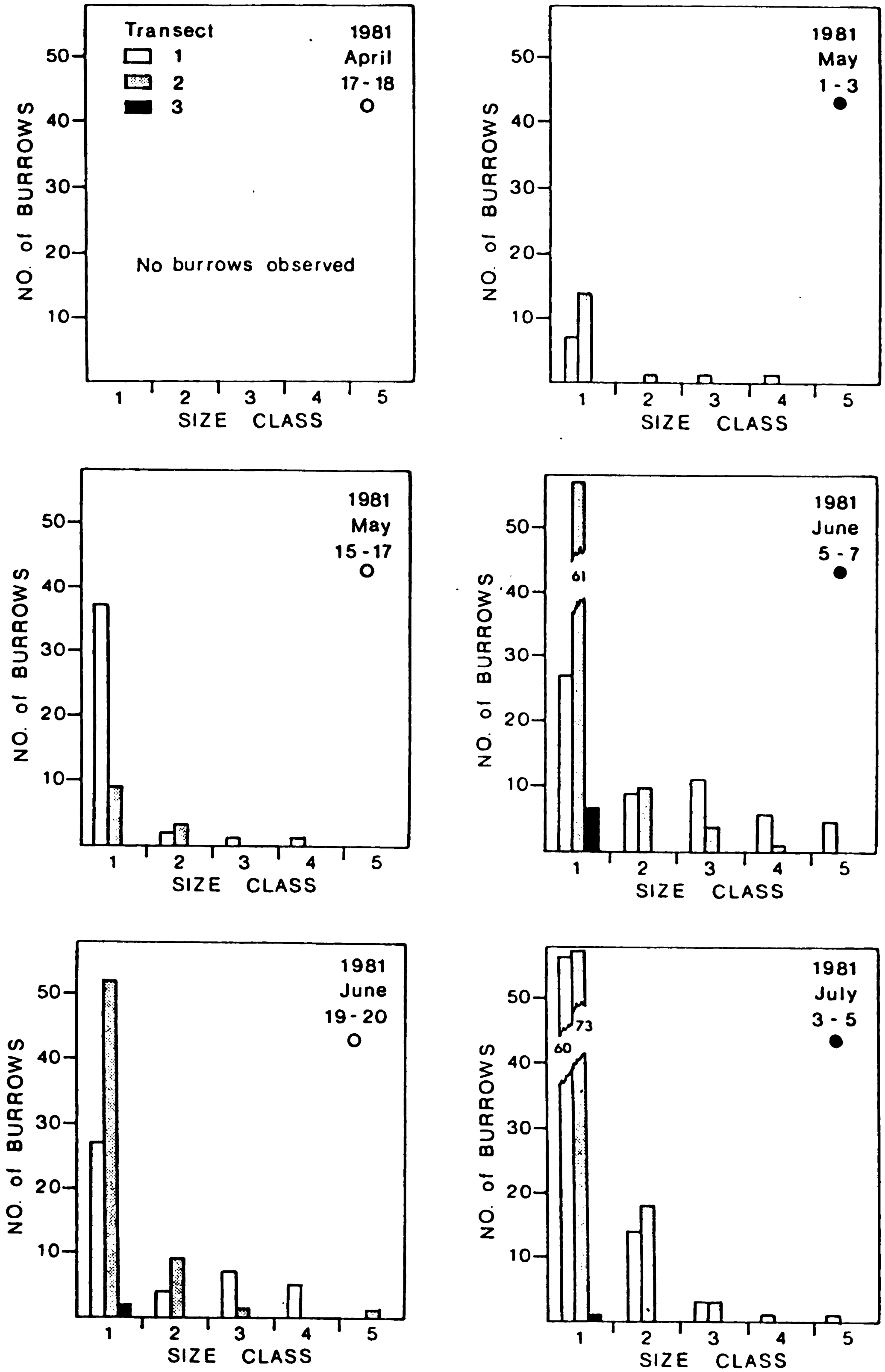

Transect
☐ 1
▨ 2
■ 3
1981
April
17 - 18
○
No burrows observed
1981
May
1 - 3
●
1981
May
15 - 17
○
1981
June
5 - 7
●
61
1981
June
19 - 20
○
1981
July
3 - 5
●
60
73
NO. of BURROWS
10
20
30
40
50
SIZE CLASS
1
2
3
4
5

Figure 20

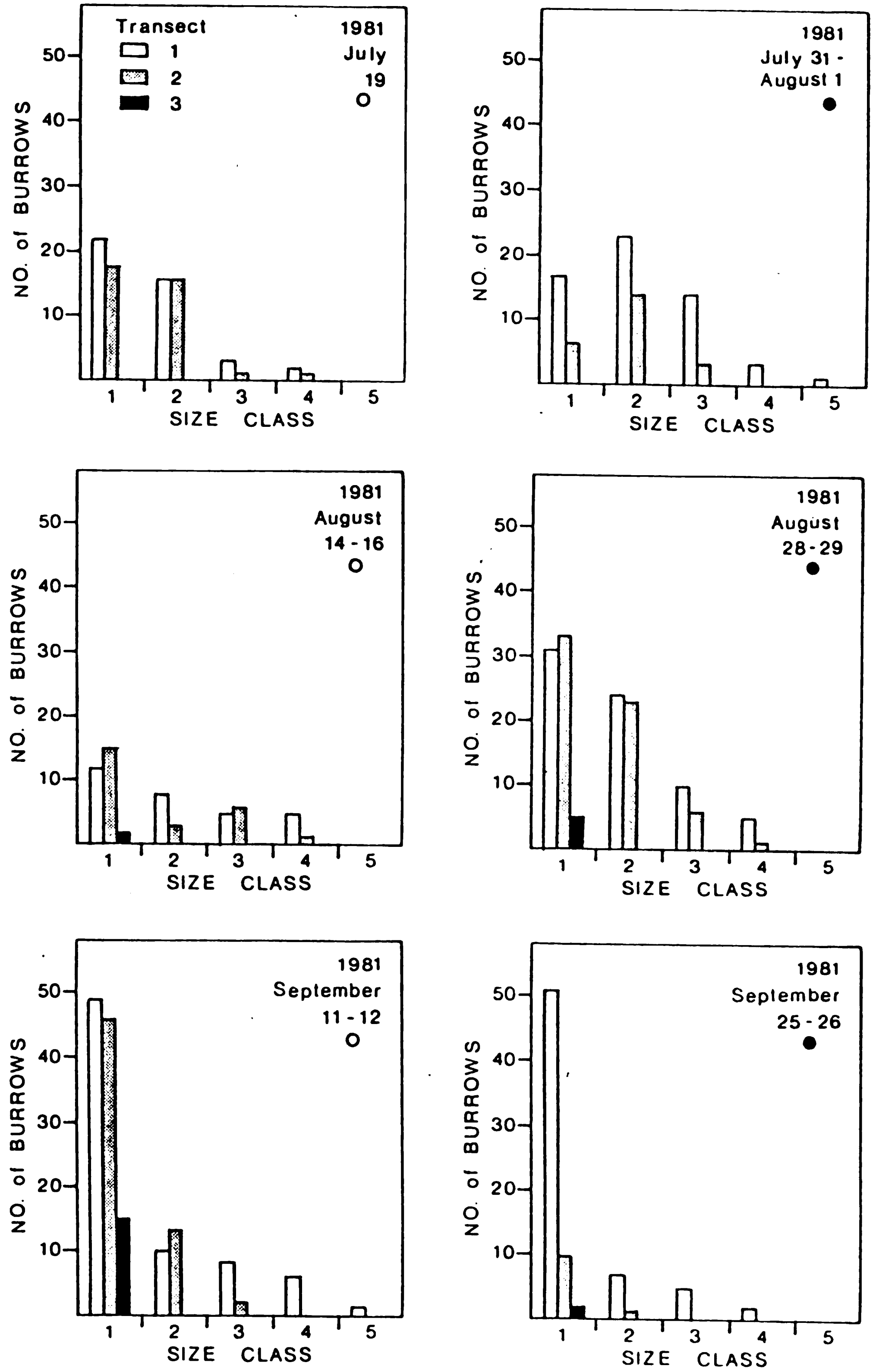


Figure 20 (cont'd.)

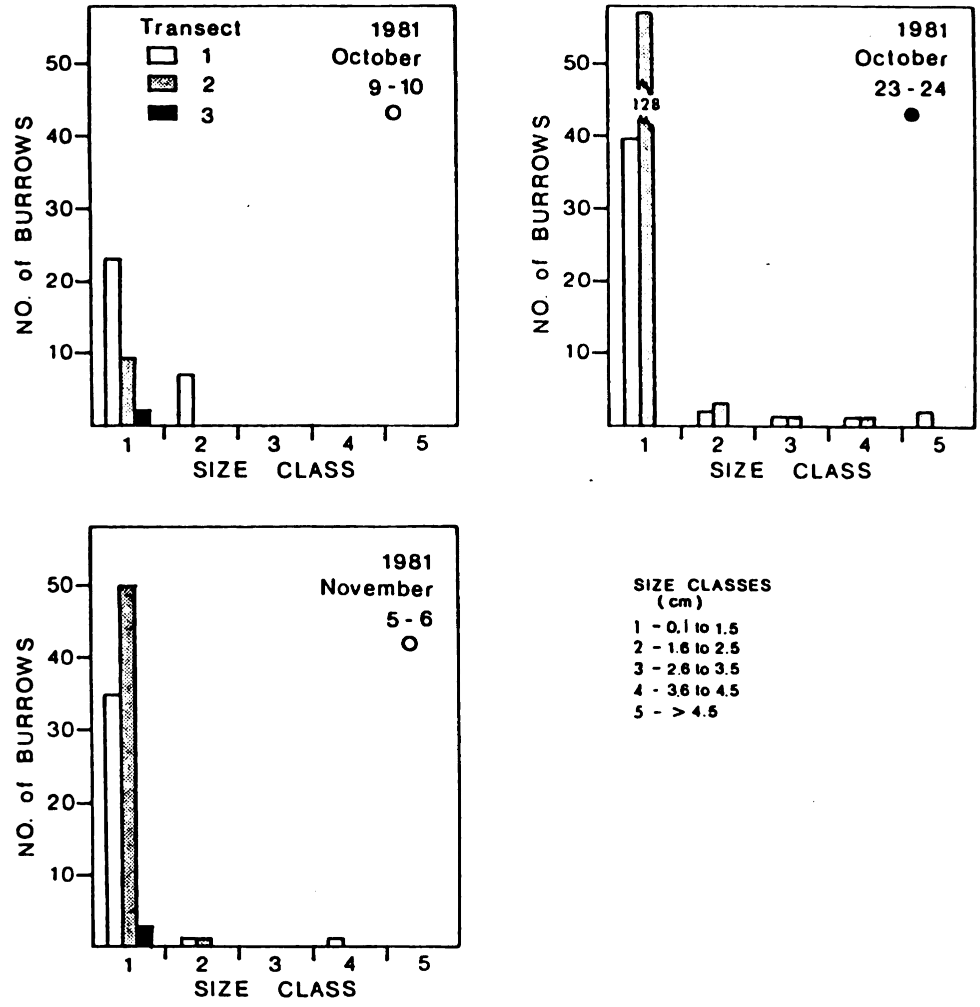


Figure 20 (cont'd.)

Figure 21 Total number of crabs (recorded by burrow count) for each transect reported by size class for each sampling period in 1982

○ Full moon ● New moon

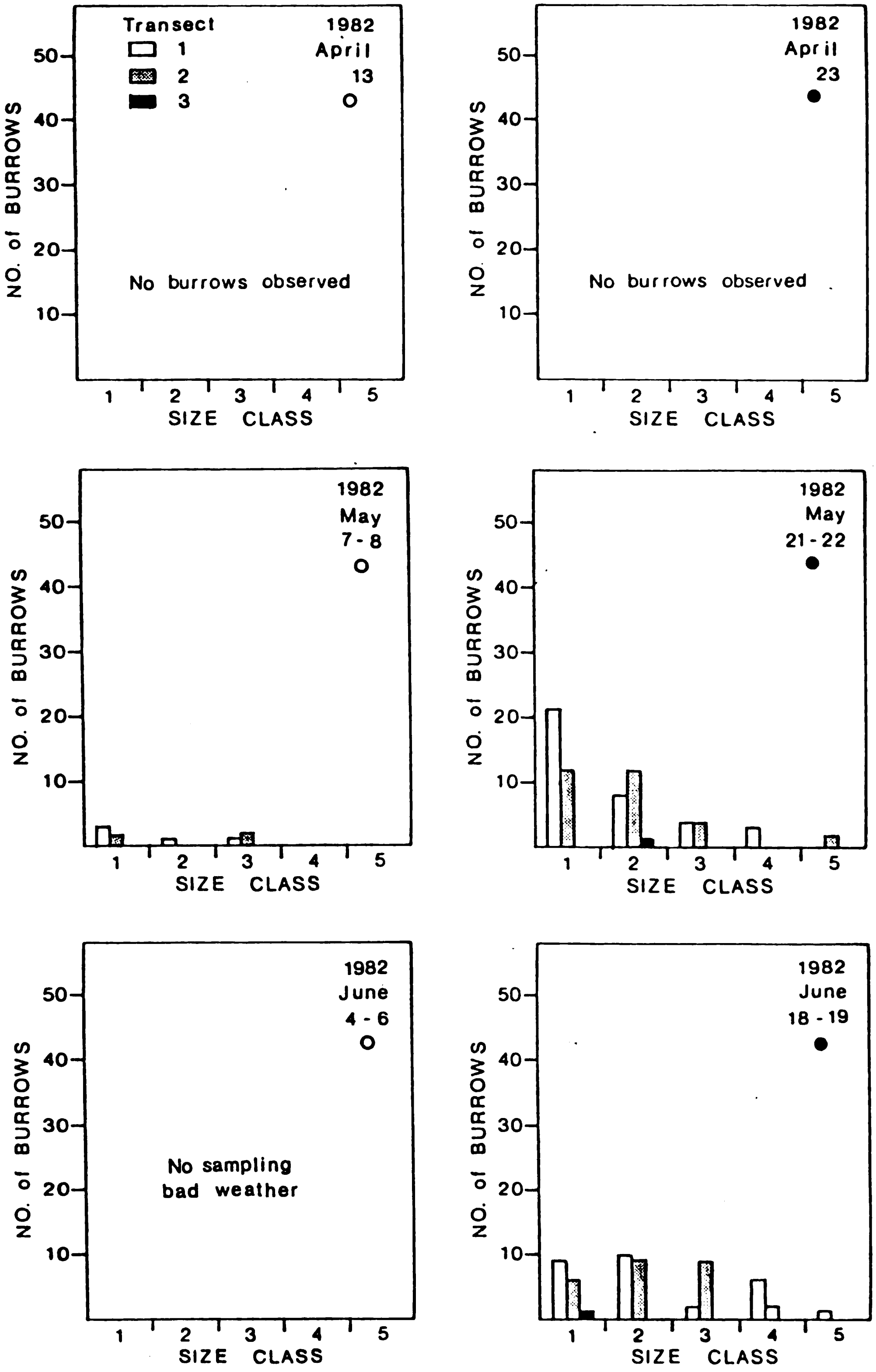

Transect
1
2
3
1982
April
13
○
No burrows observed
1982
April
23
●
No burrows observed
1982
May
7 - 8
○
1982
May
21 - 22
●
1982
June
4 - 6
○
No sampling
bad weather
1982
June
18 - 19
●
NO. of BURROWS
10
20
30
40
50
SIZE CLASS
1
2
3
4
5

Figure 21

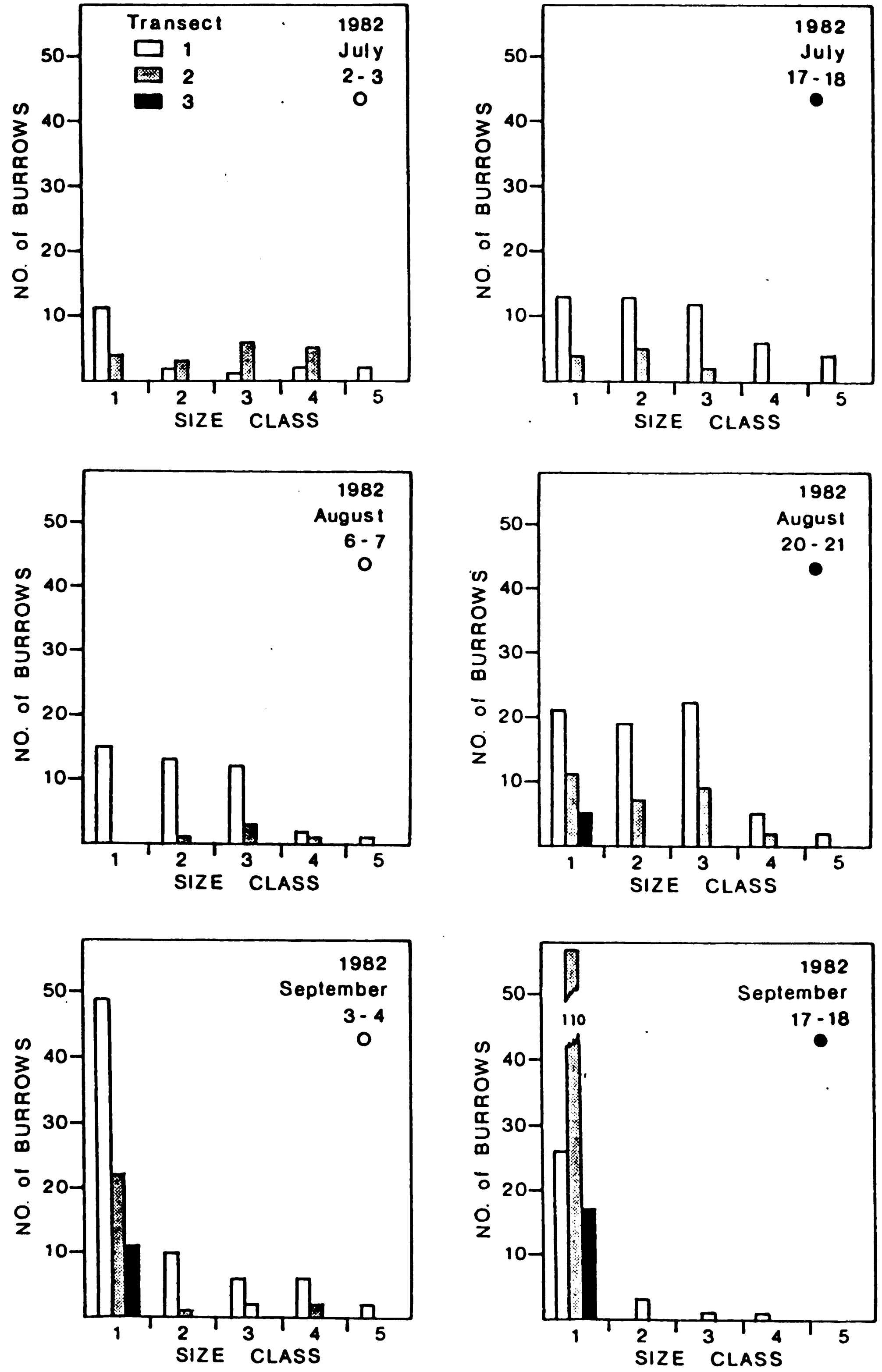


Figure 21 (cont'd.)

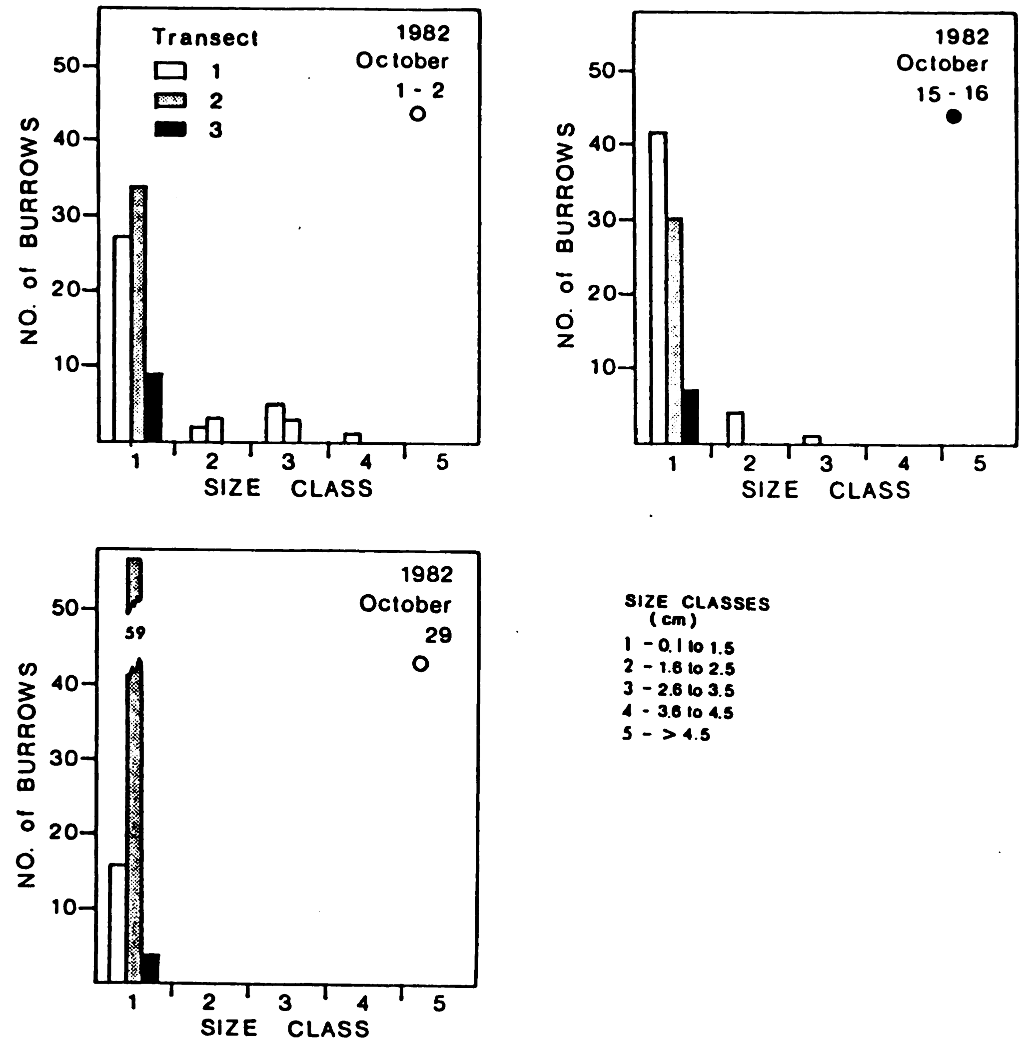


Figure 21 (cont'd.)

beaches in August would become mature. Since ghost crabs on Assateague Island were inactive for a longer period (November through April) than in Texas (January-February), the August brood should reach maturity toward the end of September of the following year. This could explain the copulatory act observed in early September 1982.

Haley (1972) reported that inseminated females with ripening ovaries were found prior to the onset of surface (beach) activity, indicating that oogenesis can initiate in overwintering females, and that spermatozoa can be retained during the dormant period. This could reduce the time to first crab by up to 45 days depending on the stage the ovaries reached prior to the female crabs' emergence on the beach.

Table 15 gives information relative to size, sex, and reproductive condition of the 106 crabs captured and measured in 1981/82.

The style and type of burrow has also been reported to influence Ocypode reproduction (Linsenmair, 1965, 1967 cited in Hughes 1973; Hughes, 1966, 1973; Jones, 1972). Construction of mounds on Assateague Island was associated with large diameter burrows. In 1981 mounds began to appear in mid-June and decreased in number in mid-September. In 1982, occurrence of these mounds showed a similar pattern with the first observation on June 18 and then a decline in abundance around September 18. However, there was a perceptable increase in mounds associated with burrows in October. Figure 22 shows this type of mound, and a sample grid showing a number of mounds. Based on visual inspection only, there appeared to be no specialized burrow form associated with these mounds. The mounds were

Table 15

Numbers of crabs measured in 1981 & 1982 indicating numbers of males, females, gravid females, moon phase and average carapace measurements

Date	NS*	NM	NF	NG	NM**	AL	AW	AD	MP
6/19/81	13	12	1	0	9	2.21	2.79	1.71	F
8/28/81	27	18	9	0	16	1.92	2.47	1.45	N
7/17/82	30	10	20	6	25	2.29	2.93	1.73	N
8/20/82	36	18	18	1	30	2.50	3.28	1.97	N
Total	106	58	48	7	80				
% Total		54.7	45.3	7	76				

* NS, Number in Sample; NM, Number of Males; NF, Number of Females; NG, Number Gravid; AL, Average Length; AW, Average width; AD, average depth; MP, moon phase

** Carapace width equal to or greater than 25 mm

Figure 22 Typical burrow mounds constructed by O. quadrata on Assateague Island, Maryland. A typical mound and its close association with its burrow; B typical sample grid with several mounds located in and around the grid

usually closely associated with burrows (Figure 22A). When crabs were observed on the mounds, they were sitting on the dune side below the summit of the mound.

Although the occurrence of mounds appeared to coincide with the reproductive period of _O. quadrata_ on Assateague Island, no relationship between the two was determined. Hughes (1973), reported that mounds were constructed by mature _O. quadrata_ males (approximately 90%) and that on a number of occasions females were found with males in the burrows. The female was most often found in the secondary branch of the burrow, with the male usually located at the bottom of the main shaft. No females were found in the burows of males during this study. Crane (1941) suggested that the "Y"-shaped burrow played a part in reproduction of _O. quadichaudii_. It is possible that "y"-shaped burrows serve this function in _O. quadrata_ as well.

Linsenmair (1965, 1967, cited in Hughes 1973), working with _O. saratan_ (Forskal), observed the role played by burrows in the courtship and copulation of this species. He reported that sexually mature males dig burrows that are different from the common burrow. These burrows spiral downward in either a clockwise or counter-clockwise direction, depending on which cheliped is larger. Sand excavated from these burrows was placed in a "pyramid like" pile about 20-50 cm from the burrow entrance. Linsenmair (1967, cited in Hughes 1973) reported that copulation takes place within these burrows. "Sand pyramids" stimulated other males to build similar burrows, as well as to attracted females to the burrow. This obviates the need for males to actively display in areas where populations were active by day. Hughes (1973) re-evaluated his earlier work (Hughes, 1966) concerning *O. ceratophthalmus* on Inhaca Island, Mocambique, and concluded that this species digs copulation burrows similar to those constructed by *O. saratan*. He also reported that non-spiral burrows may be occupied by either sex. He examined over 100 copulation burrows and, in each case, the burrow was occupied by a large, sexually mature male. Based on the examination of males and females found in *O. saratan* burrows (Linsenmair, 1967 cited in Hughes 1973) and his own extensive observations on *O. ceratophthalmus*, Hughes concluded that these two species copulate within their burrows. This, however, conflicts with the observations of Letterman (1973).

Letterman (1973), while reporting the occurrence of spiral burrows for *O. ceratophthalmus*, stated that they were constructed by both males and females. He postulated that they appeared easier to defend than straight burrows. He also suggested that since Green Island, N.Q., Australia, was a coral cay, the spiral burrow might be an attempt to obtain a burrow length similar to those possible in pure unobstructed sand. Jones (1972) reported that spiral burrows, with associated sand pyramids, were constructed by *O. kuhlii* de Haan. He reported that the burrows with pyramids were constructed only by males. The females scattered the sand around their burrows in an arc so that it remained inconspicuous.

de L. Brooke (1981) studied the relationship between size and ownership of copulation burrows in *O. ceratophthalmus* on Cousin Island, Seychelles. He found that large males were able to defeat smaller males and to build their copulation burrows in the best locations. He was, however, unable to detect any relationship between size of males and distance to the nearest copulation burrow. Takahasi (1932), on the other hand, stated that the distance between burrows was correlated with size of neighboring crabs. Hughes (1966) reported a defended area surrounding a burrow of O. ceratophthalmus. Linsenmair (1965, 1967, cited in Hughes 1973) stated that sand pyramids had a repulsive function which served to space adult male burrows a minimum of 134 cm apart in O. saratan. Although no specific effort was directed toward determining the relationship between burrow size associated with a mound and distance to its nearest neighbors, review of raw data collected during this study do not support such a relationship. Sometimes burrows tended to be randomly distributed within sample grids, while at other times burrows were clumped. He also noted the filling of an adjoining burrow of O. saratan by an adult male neighbor. Burrow filling has been reported for O. ceratophthalmus by de L. Brooke (1981) and Lighter (1974) and for O. gaudichaudii in Crane (1941). Lighter suggested that both pyramid building and burrow filling may play important roles in spatial distribution, with pyramids serving as territorial "sign posts". During 2 years of observation no burrow filling was observed on Assateague Island.

Stridulation has been linked to reproductive activity in ghost crabs. Ocypode spp. are unique among crustaceans, in that all but one species possess a specialized stridulatory organ on the cheliped (Horch, 1975). O. cordimana is the only member of the family without a stridulatory organ.

Stridulation takes place when the crab rubs a transverse row of tubercles (found on the inner surface of the palm of the larger cheliped) against a ridge on the ischiopodite of the same limb. However, during two years of study on Assateague Island, stridulation was never observed or heard. Similar results for O. quadrata were reported by Milne & Milne (1946) and Cowles (1908).

O. quadrata can perceive high frequency air-borne sounds and substrate vibrations (Horch and Salmon, 1969). Other Ocypode species responded to both air-borne and substrate-borne sounds (Horch, 1971; Horch and Salmon, 1972). Horch (1974) identified Barth's myochordotonal organ as the receptor responsible for this sensitivity.

Other members of the family apparently utilize stridulation more frequently than O. quadrata. de L. Brooke (1981) reported that the sound produced by O. ceratophthalmus could be heard for a distance of 5 m. He also stated that he frequently observed male members of this species making stridulatory movements at the entrance to their burrows. The males were located just below the surface of sand with their backs pressed against the outer (i.e., greater radius of curvature) wall of the spiral burrow with the larger cheliped closer to the entrance. Hughes (1973) noted that day-active males on Inhaca Island were not heard to stridulate, but that nocturnally active males were, and that this stridulation took place immediately within the mouth of the burrow. de L. Brooke (1981) speculated that stridulation may have a function analogous to bird song, i.e., to attract females and/or to deter intrusion by conspecifics.

Horch and Salmon (1972) stated that frequency of stridulation in O. ceratophthalmus appeared to show a periodicity related to the phase of the moon similar to burrow building. The period just before the new moon, when the greatest number of copulation burrows were being built, was also the time when male crabs were most likely to be heard stridulating within the burrow (Horch and Salmon 1972). However, Horch (1975) stated that the exact social significance of acoustic signaling in these species (O. cordimana and O. ceratophthalmus) is unknown. Thus, while most, if not all, Ocypode produce some acoustic signal, what function it serves is as yet not understood.

Visual displays may also play a role in attracting a mate, or in defending a copulation burrow or territory. However, no evidence was found during this study to indicate that mounds constructed by O. quadrata were used either as a visual clue or territorial marker. While crabs were found sitting on the upper rear side of the mounds, they made no observed displays.

Agonistic displays were observed on the beach and in conjunction with disputes over burrows on numerous occasions during this study. Whether or not displays were a confrontation involving a burrow or an interaction on the beach, they commonly took the following form: both crabs raised themselves on their legs facing each other, the chelipeds held apart with the tips pointing downward or downward-forward. The crabs may remain in this position for some time, after which they walked away with chelae lowered to the normal position. On a number of occasions two crabs actually made contact with the chelae and pushed. Following the push, which was usually very short, the crabs would part and one or both would walk away. In disputes involving burrows, the victor usually remained with the burrow. No instance of actual grabbing with the chelae was ever observed. These observations were similar to those reported by Schone (1968), Wright (1968) and Letterman (1973).

Schone (1968) stated that within the family _Ocypodidae_ behavioral patterns linked to sexual interactions have been observed largely in fiddler crabs of the genus _Uca_. The cheliped-waving of males and other forms of display have been well described. There appears to be no similar form of display within the genus _Ocypode_ except for the ritualistic encounters previously described.

Finally, air-borne chemical signals could play a role in _Ocypode_ reproduction. Trott and Robertson (1984) demonstrated that _O. quadrata_ could detect chemical stimulants placed on the cheliped. Stimulants extracted from food sources were used, and demonstrated the crabs ability to detect chemical stimulants. These receptors might detect an air-borne chemical cue. This could be a possible explanation of the mechanism involved in the detection of the female crab observed in the copulatory event in 1981. In addition, it could also explain the quick response of the male crabs noted in laboratory observations by Hughes (1973).

A comparison of reproductive behavior between _O. quadrata_ on Assateague Island, Maryland and populations to the south indicates a substantial similarity. In both areas copulation was accomplished in a similar fashion on the open beach. Although the copulation period on Assateague appears shorter than the southern populations, this was to be expected since Assateague Island is near the northern limit of _O. quadrata's_ range. Mounds were associated with larger burrows in both locations, but not conclusively linked with reproductive activity.

Recruitment

No data were collected on abundance of O. quadrata zoeae and megalopae in the adjacent ocean; recruitment was therefore inferred from relative abundance of size class 1 crabs (0.1-1.5 cm).

To aid in this effort, a ratio was developed by summing the number of crabs present in the four larger size classes (2 through 5) and dividing it by number of crabs in the first size class. These data are graphically displayed in Figures 23 and 24. Transect 3 was not included in the graphs because its ratio was always zero. Figures 20 and 21 show the total number of crabs in each of five size classes by sample date for each transect in 1981 and 1982, respectively.

Analysis of these data indicated bimodal recruitment in 1981, with an initial peak of activity beginning in early June and a second major wave of recruitment occurring from mid August to early November. In 1982 there was some evidence of an early recruitment period in the June/July time frame, but data were inconclusive. The major recruitment period began in late August and extended until the end of October. Data for transect 3 (Figures 20 & 21), show these patterns quite clearly. These burrows were almost all under 1.0 cm in diameter and located within the area overwashed by the most recent high tide.

These time frames for recruitment agree with Grant (1979) reporting on O. quadrata in the neuston off New Jersey and Virginia in August, and Smith's (1873a, 1873b) reports on the finding of O. quadrata on the beach at Fire Island, New York in late August of 1870. Smith (1873a) stated that they were common on the outer beach by mid-September. Haley (1972) reported that in Texas, O. quadrata

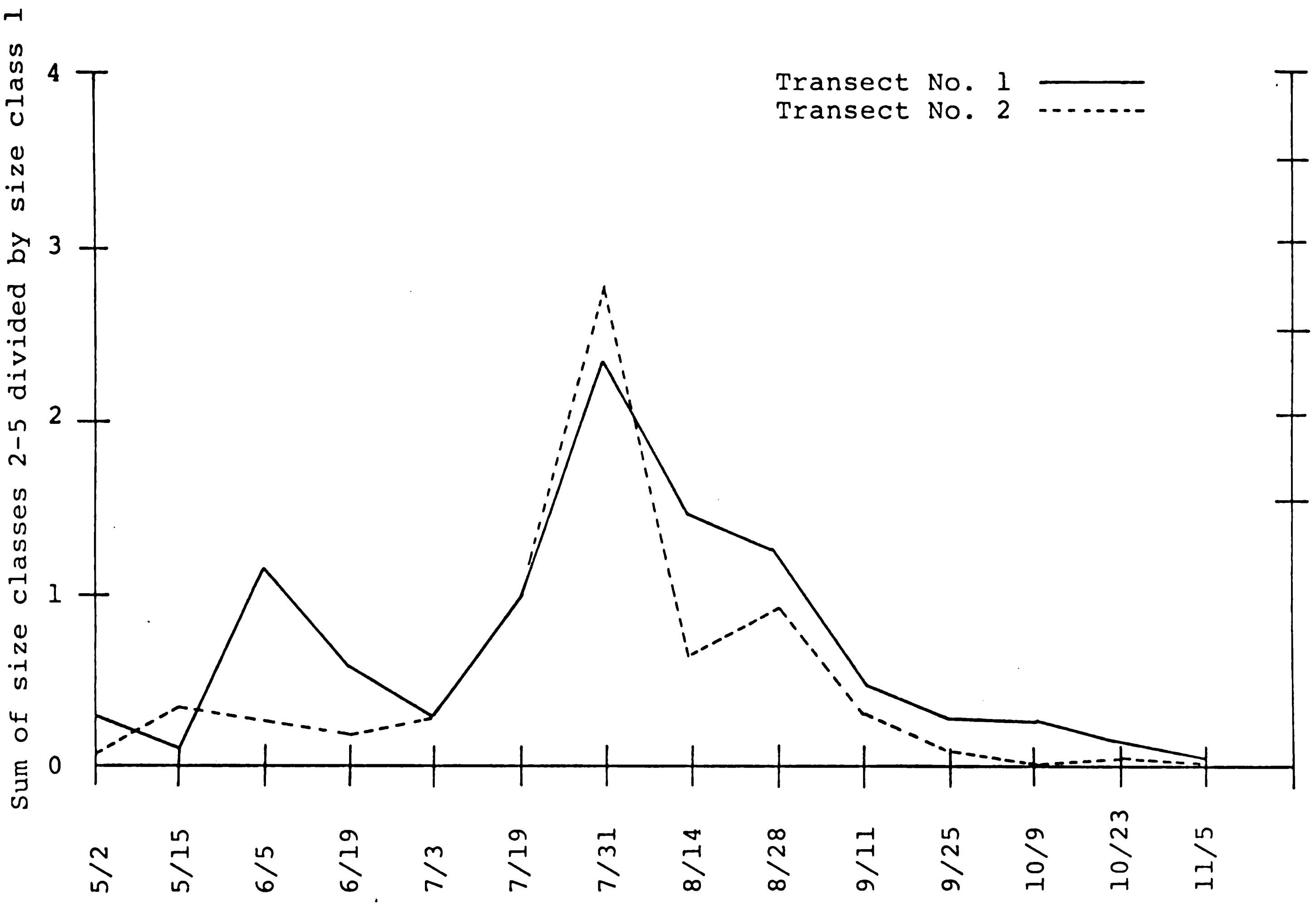


Figure 23 The ratio of the sum of size classes 2-5 divided by size class 1 plotted by date for transects 1 & 2 in 1981

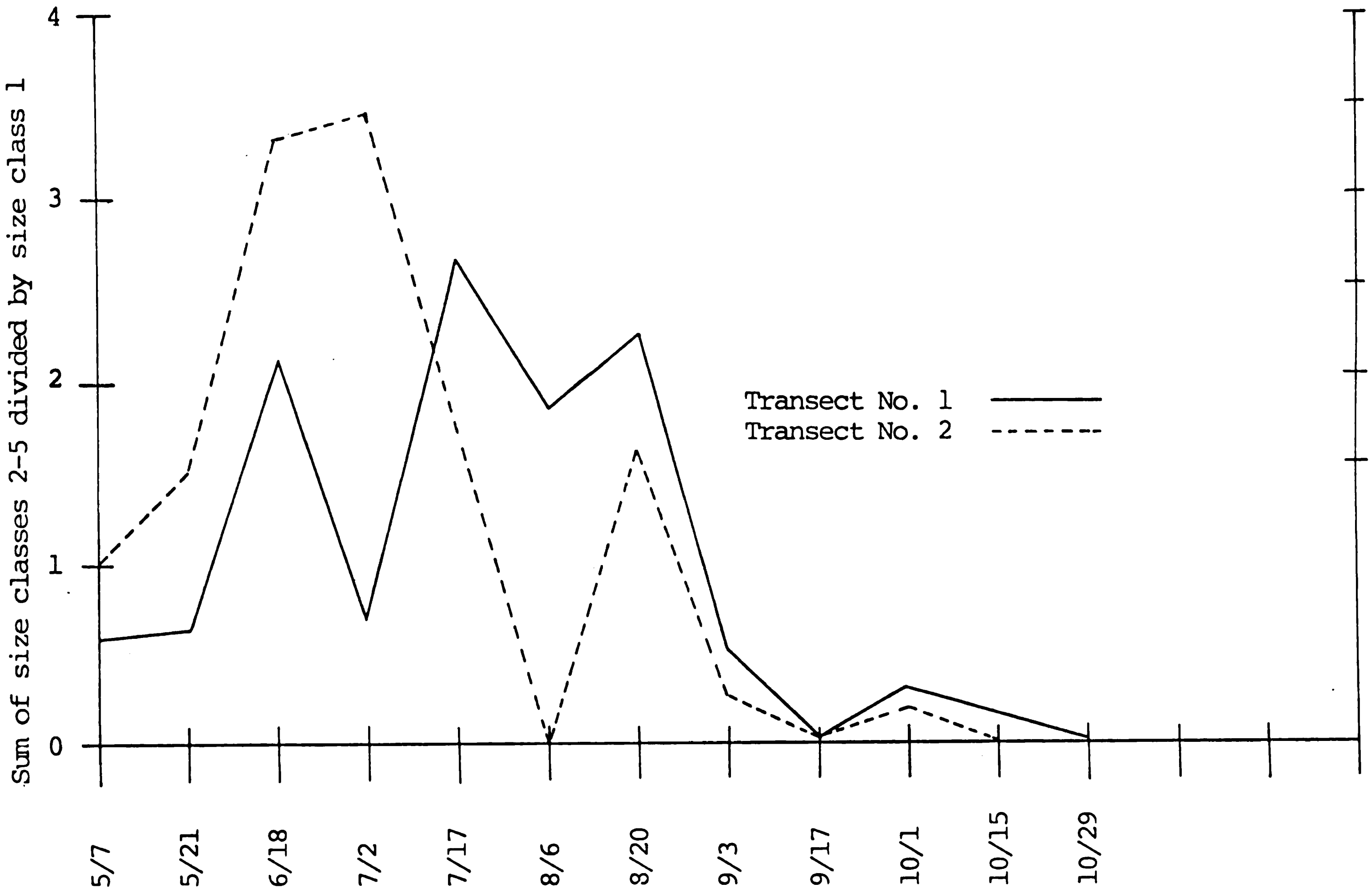


Figure 24 The ratio of the sum of size classes 2-5 divided by size class 1 plotted by date for transects 1 & 2 in 1982

was recruited to the beach in May and August. Coues (1871) noted young first appearing around the latter part of April at Fort Macon, North Carolina. Allowing for the more northern location of Assateague Island, and the fact that cooler temperatures during development retard larval development, recruitment periods noted on Assateague appeared to fall within the reported range (Figures 20 & 21).

New recruits arrived on the beach during October/November, even though the calculated size ratio (sum of 2-5) was affected by seasonal emigration of larger crabs to areas behind the dunes. Increased crab activity behind the dunes was observed in both 1981 and 1982. Figures 20 and 21 show reduced numbers of adults on the beach during this period. Thus, in the fall and especially in the last few sampling periods, the population consisted almost entirely of size class 1. In fact, raw data showed that, in these latter sampling periods, the vast majority of burrows were 1.0 cm in diameter or smaller, with many in the 6.0 to 7.0 mm range. Based on the size of first crabs (carapace measurememts of 5.6 to 6.0 mm long and 6.1 to 6.5 mm wide when crabs first appeared on the beach) on Fire Island reported by Smith (1873a), burrows of this size can be attributed to new recruits.

The exact mechanism by which _O. quadrata_ is recruited to or retained on Assateague Island is not well understood. Recruitment was almost continuous from May through November in both 1981 and 1982 (Figures 25 & 26). Since resident adult populations would not be in reproductive condition so early, this level of recruitment suggests a major spawning population outside the Assateague area. Larval forms are planktonic and, therefore, both surface and sub-surface current patterns along the east coast are likely involved. Two mechanisims,

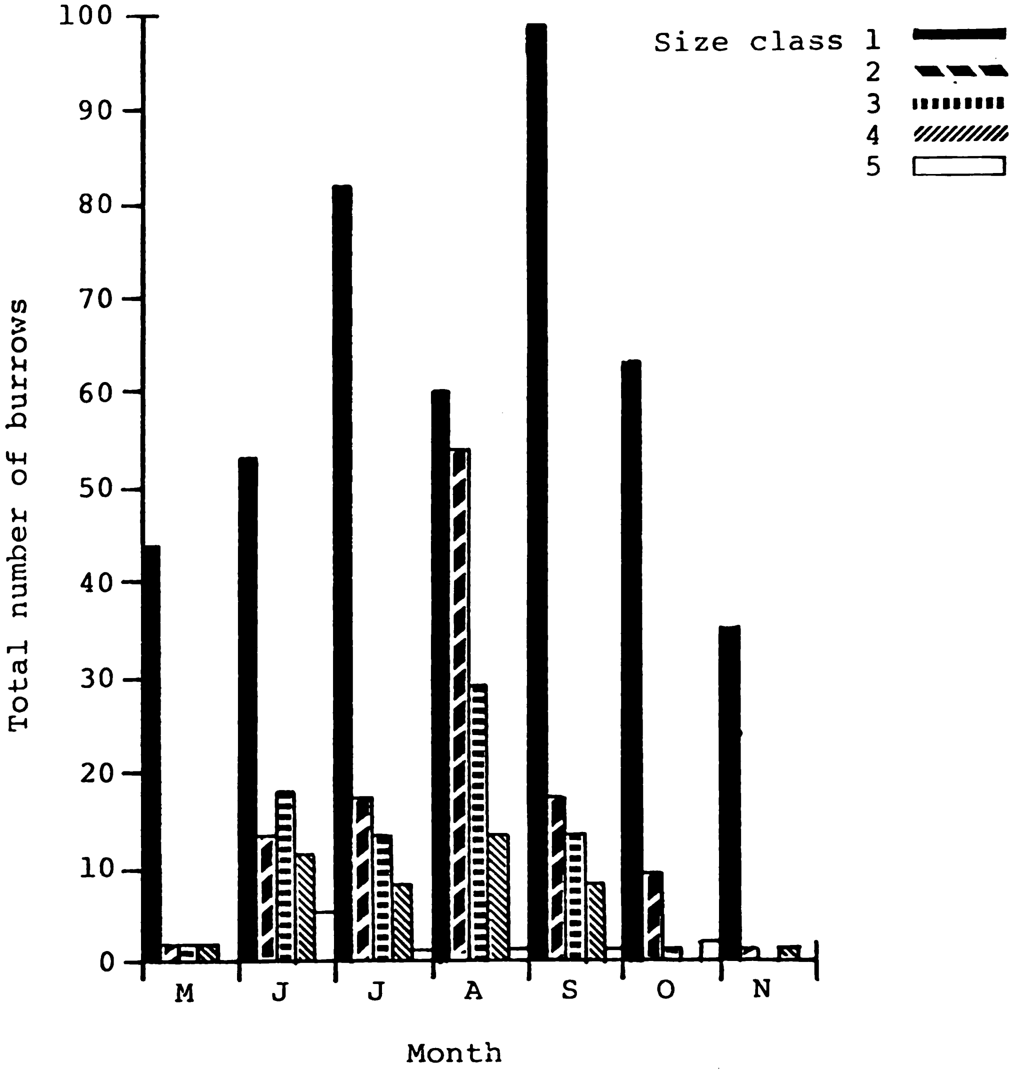


Figure 25 Total number of crabs (recorded by burrow counts) by size classes by month for transect 1 for 1981

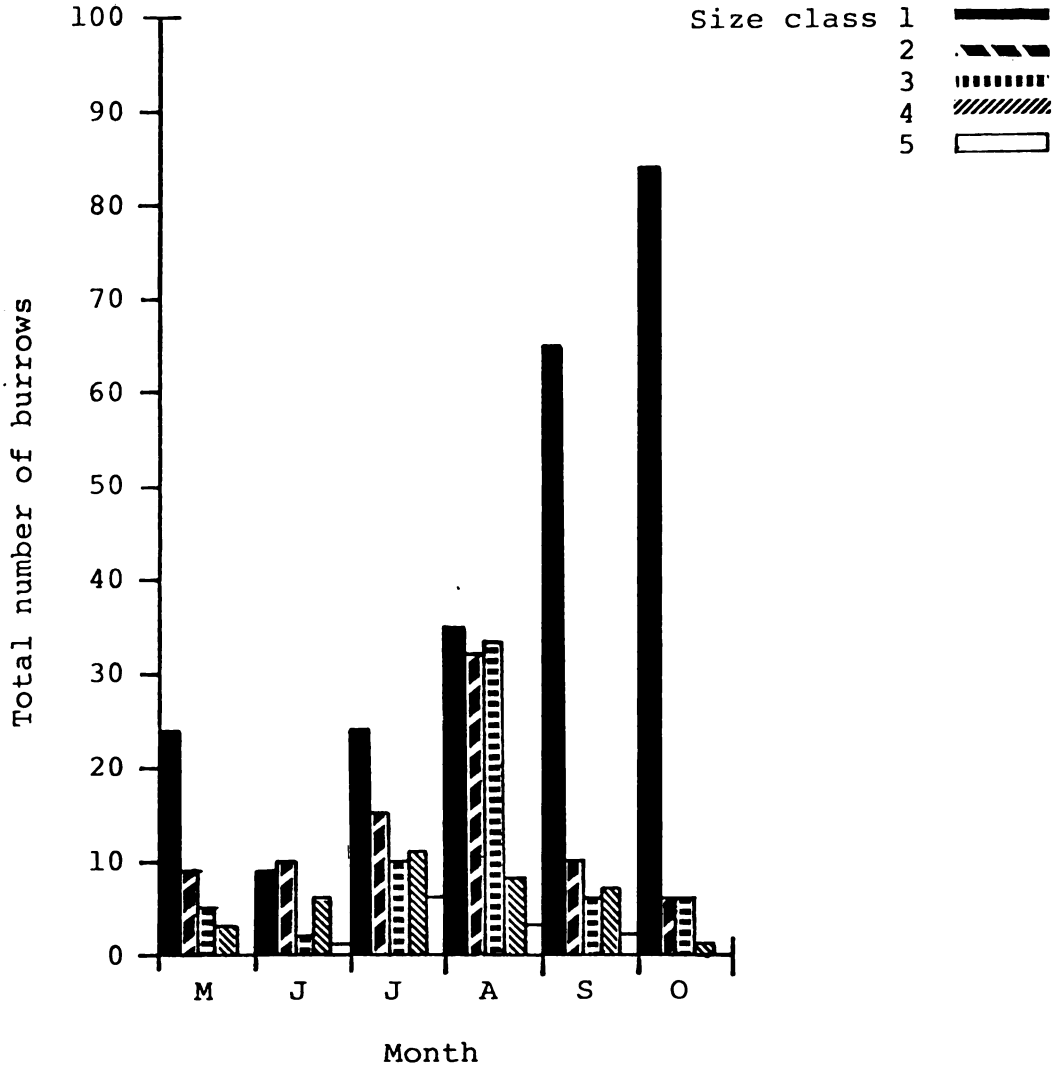


Figure 26 Total number of crabs (recorded by burrow counts) by size classes by month for transect 1 for 1982

postulated by Efford (1970) for recruitment of E. analoga, appeared to be possible: (1) counter current hypothesis; and (2) gyral hypothesis.

The counter current hypothesis may be satisfied by the south-flowing Virginian Current (shelfwater mass) moving along the coastline bounded on the outer edge by the north-flowing Gulf Stream (Figure 27). There is also an onshore drift on the seafloor along the Atlantic Coast between the Bay of Fundy and Southern Florida (Scheltema, 1975). Lee (1975) reported that there was mixing between these two major currents and that spin-off eddies along the western boundary of the Gulf Stream were regular features. Smith & Jossi (1984) reported that the frequency of Gulf Stream eddy passage through the New York Bight corresponded with the frequency of tropical-subtropical net phytoplankton in their samples. Plankton moved into the outer shelf by Gulf Stream eddies were moved to the inner shelf by wind-induced currents moving up the Hudson Shelf Valley. Therefore, larvae may be transported northward by the Gulf Stream and then southward by the Virginia Current. Shoreward movement could then be enhanced by onshore drift along the seafloor.

The gyral hypothesis requires the presence of spin-off eddies noted by Lee (1975) to move larvae back near shore. Since this activity takes place in the Gulf Stream and not the Virginia Current, there would be limited opportunity for larvae produced north of Cape Hatteras to enter this system. However, since the Virginia Current routinely flows into the zone seaward of Cape Hatteras, and is eventually absorbed (Ford & Miller, 1952), it is possible that larval forms of O. quadrata produced north of Hatteras enter the system at

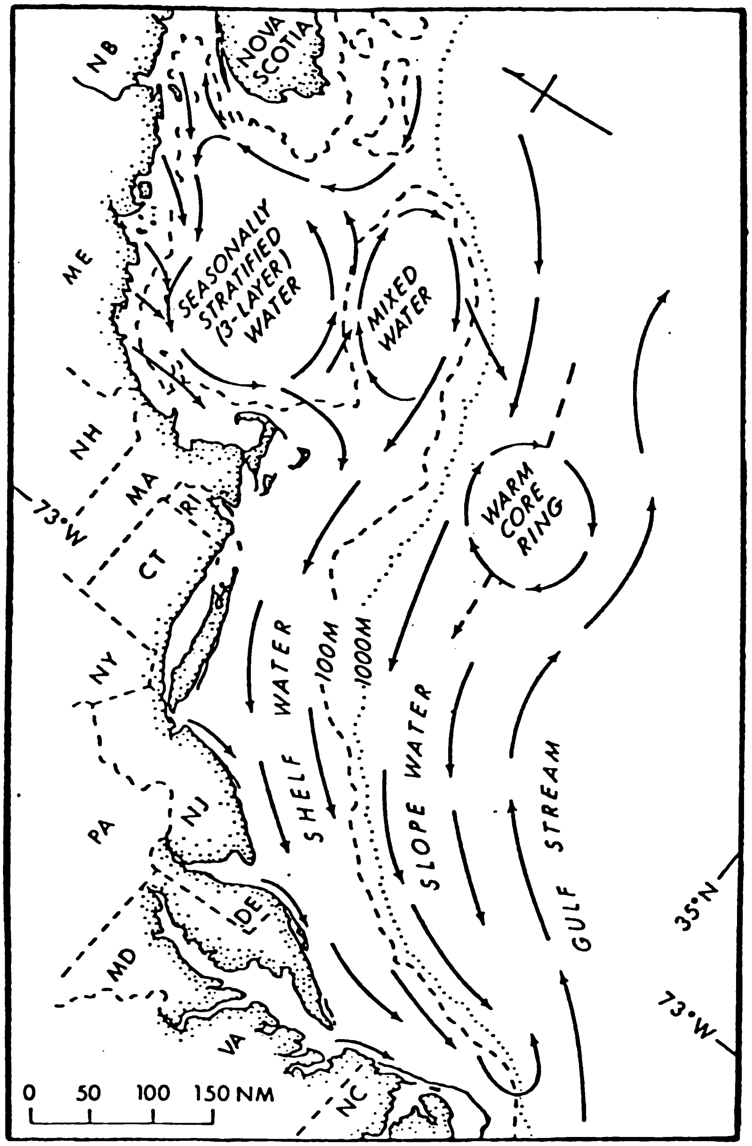


Figure 27 General surface layer circulation of northwestern Atlantic coastal and offshore waters. (From Ingham, 1982)

this point.

Recruitment and retention of O. quadrata may occur as a result of a combination of gyral and counter current mechanisms. Larvae produced along the northern coast (New Jersey to northern North Carolina) would be transported south in the Virginia Current where they would be swept shoreward by the bottom current in this area to repopulate the beaches to the south. Larval forms not reaching a beach during their initial southern movement could be moved out to sea off Cape Hatteras and entrained in the Gulf Stream. Larvae produced along the southern coast (southern North Carolina to Florida) may be entrained in the Gulf Stream and carried north where spin-off eddies and wind-induced currents would then transfer them into the south flowing Virginia Current.

Williams (1974) attributed the northern-most occurrences of tropical crabs of the genus Callinectes to drift of larvae entrained in currents associated with the Gulf Stream. Thus, if these southern species can be transported to the north, it is also quite possible that O. quadrata could be carried north with the Gulf Stream. Cowles (1908) reported that Verril proposed the Gulf Stream as the source of O. quadrata which he captured near Block Island, Rhode Island. Smith and Jossi (1984) reported an increase in the frequency of occurrence of tropical-subtropical net phytoplankton in their samples corresponded to the frequency of Gulf Stream eddies.

The duration of transport is critical for larval survival and ultimate deposition on mid-Atlantic beaches. Diaz & Costlow (1972) found that in the laboratory, a minimum of 34 days from hatching was required for the megalopa stage of O. quadrata to appear. Data developed by Costlow & Fagetti (1967) for C. cinereus, showed that 20 days were required to reach first crab stage from the megalopa. Adding these figures provides an estimated value of 54 days from hatching to first crab stage. Therefore, the ghost crab spends approximately 55 days as a component of oceanic plankton before being deposited on the beach as a first crab stage.

Larvae released into the ocean on Assateague Island must travel 322 km south to Cape Hatteras before entering the Gulf Stream. The southward moving current (Virginia Current), which would transport these larvae, moves southward at about 5-10 cm/sec (Ingham, 1982). Using an intermediate value of 7 cm/sec, it would take the larvae about 53 days to reach Cape Hatteras. It is unlikely, therefore, that very many O. quadrata larvae produced from Virginia northward would be deposited on Assateague Island. Those entering from Virginia southward would take approximately one-half the time, or about 26 days, to reach Cape Hatteras. They would then be transported to the north by the Gulf Stream. The larvae would be moved to the north on the surface at an average speed of four knots (Gross, 1972) and would cover the distance of 483 km to New Jersey in 4 days, prior to being entrained in a spin-off eddy and being returned to the south-flowing Virginia Current. It would then take approximately 26 days for the larvae to be transported 161 km miles south to Assateague Island. Larvae originating from Assateague Island would require about 83 days to return to their place of origin. Those from south of the mouth of Chesapeake Bay to Cape Hatteras could make the trip in about 56 days or less. The times given for reaching the first crab stage are most likely minimal. Thus, a considerable number of larvae could survive and be deposited as first stage crabs on Assateague Island. This theory tends to be supported by Grant (1983) who reported that only immature specimens are regularly found on the beach at Sandy Hook, New Jersey, where *O. quadrata* was near its northern limit and does not successfully over-winter.

Vertical distribution of larvae in the water column also must be considered. Grant (1979) noted that all megalopae of *O. quadrata* were taken from surface neuston tows. Since tows were taken both during the day and at night, and larvae were found only in the surface tows, the larvae are probably not phototrophic. Response to gravity, or geotaxis, has been reported as one of the behavioral mechanisms utilized by *C. sapidus* (Milikin & Williams, 1984). Megalopae of *O. quadrata* may be negatively geotactic which could account for their occurrence in surface layers. Current speeds tend to be higher at the surface and, thus, could hasten the distribution of *O. quadrata* megalopae throughout their range. Salinity and temperature also tend to be higher near the surface. *O. quadrata* may be physiologically adapted to higher salinities and temperatures which would tend to maintain the megalopa in the surface layers. In addition, increased salinity extends the average duration of the megalopae stage of *C. sapidus* (Milikin & Williams, 1984). It might have a similar influence on *O. quadrata*. There appeared to be no relationship between the arrival of recruits on the beach and moon phase (Figures 20 & 21 pages 74 & 78).

Data obtained during this study indicated that maximum recruitment of size class 1 (0.1-1.5 cm) crabs occurred during September and October in 1981 and 1982. Recruitment in Texas has been reported to occur in late July-early August, with young beginning to appear in North Carolina in the latter part of April. Given the cooler temperatures and shorter activity period found on Assateague Island, the approximately one month delay in maximum recruitment compared to the Texas population appears reasonable. Since since class 1 crabs were found on the beach in May, the April date for North Carolina also appears to be within reasonable limits. Thus, recruitment on Assateague Island, Maryland appeared to be similar to populations to the south.

Lunar rhythms in reproductive activity and recruitment have been well established in numerous aquatic invertebrates (McDowall, 1969). However, no conclusions could be drawn on the impacts of lunar cycles on *O. quadrata*.

Growth

Growth was not measured during this study. However, some inferences can be drawn relating to the growth of *O. quadrata* on Assateague Island during 1981 and 1982.

Burrow diameter approximates carapace width (Fisher and Tevesz, 1979; McLachlan, 1980). A review of the size class data from month to month showed the relative growth of the population. Figures 25&26 (pages 95 & 96) show the five size classes (total number of burrows) plotted by month for transect 1. Since there were various human uses at the other transects which may have biased the crabs' growth rate, data from those locations were not used.

When utilizing these figures to calculate growth, one must keep in mind: (1) that the data for May are incomplete, since not all crabs have emerged from their winter dormant period; (2) data for

October-November are also incomplete because the crabs had begun to move behind the dunes and to sequester themselves in burrows in preparation for overwintering. Size class 5 (>4.6 cm) crabs were not present in May of both years, but were present in June, lending support to the theory that some crabs remain dormant until early summer. There were also a limited number of crabs in size classes 2 through 4 in 1981. In 1982, the May data showed a more uniform size class distribution, indicating a more even emergence. Air temperatures during these two periods (1981-1982) were similar. No explanation for delayed emergence is immediately obvious. Rao (1966) states that the removal of temperature stress stimulates proecdysis. This could explain the early growth increment observed in June 1981, however, growth was most likely a combination of removal of temperature stress and emerging crabs.

The burrow size data collected between June and August do not encompass early and late seasonal variations, and thus allow some general statements relative to growth of the population. A trend toward increased numbers of crabs in each of the successively larger size classes from June through August was noticed (Figures 25&26). This trend was particularly evident in 1982, with the exception of size class 5 in general, and size class 4 in August. Size class 5, in both 1981 and 1982, generally showed very low burrow counts, with the exception of June 1981 and July 1982 when counts were at least double those of any other month. These data do not provide information on individual growth, but they clearly show shifts in population size structure.

A second source of information on growth was obtained from crabs captured for the mark and recapture effort. These data are displayed in Table 15 (page 83). The percentage increase in size was calculated utilizing the information from 1982 because of its larger sample size and because maximum growth was observed in July and August of that year (Figures 25&26). Carapace width increased by approximately 12%, length by 9.2% and depth by 13%. This increase in size was substantially lower than that reported by Rao (1968) for O. macrocera H. Milne-Edwards and O. platytarsis (16-20%). Using this percentage growth (12%) instead of the 20% assumed by Haley (1972), it would take 12 moults for O. quadrata to reach the 25 mm carapace width instead of 7. It would take 420 days, assuming 35 days between moults, for a first crab of 7.0 mm carapace width to become sexually mature. If we further assume that no growth takes place over the winter dormant period (November-April), then first crabs arriving on Assateague on July 1 would not become sexually mature until about the middle of August of their second full year on the beach. Crabs arriving on the beach before or after July 1 would become mature proportionally sooner or later. Thus, the female crab in the copulating pair observed on June 6, 1981 may have overwintered as a size class 1 crab and emerged on the beach in April/May of 1979.

Environmental conditions can influence growth in crabs (Rao, 1966; Nagabhushanam and Rao, 1967) with low temperatures prolonging the duration of proecdysis (Rao, 1966). Temperature may be the critical element in the growth of ghost crabs on Assateague Island, considering O. quadrata is approaching the northern limit of its range. As a result the ghost crab's activity period was reduced compared to its southern counterparts, and its sources of food were not as plentiful. Both of these factors could cause a reduction in the rate of growth.

A similar situation was reported by Fusaro (1978) for *E. analoga*. He observed that mole crabs on Santa Cruz Island, California, grew at about 1/3 the rate of those on the Santa Barbara coastline only 42 km distant. Mole crabs experienced colder water on Santa Cruz Island than mainland. Island waters were poorer in suspended solids. Mole crabs on Santa Cruz Island (Fusaro, 1978) also moulted about one-half as often as the mainland population. Fusaro (1978) stated that if a fixed size at maturity was assumed, the island population would take about three times longer to reach that fixed size. These differences in conditions between Santa Cruz Island and the mainland are similar to conditions that exist between Texas Ghost crab populations studied by Haley (1972) and ghost crabs on Assateague Island. Data collected on Assateague suggest that an analogous difference in time to maturity (420 days vs. 245 days) exists between populations of *O. quadrata* on Assateague and the Texas coast.

Data obtained during this study suggests that on Assateague Island, Maryland, *O. quadrata* has a smaller percentage growth (12%) and consequently requires more moults and time to reach maturity than the Texas population. This apparent difference between northern and southern populations could be the result of the reduced growing season near the northern limit of *O. quadrata's* range and/or dietary differences. Further controlled laboratory experimentation is required to determine if these apparent differences are real.

Burrow Construction

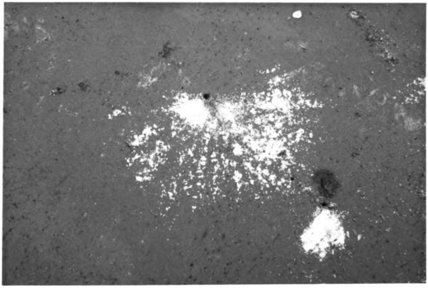
On Assateague Island, O. quadrata constructed three types of burrows; the "Y"-shaped, unbranched tunnel (straight, slightly-arched or "J"-shaped) and "U"-shaped. The "Y"-shaped and unbranched burrows were the most common types with the "U"-shaped occurring infrequently. No data were collected on the size or sex of the individual burrow occupants because they were usually encapsulated in the casting. Burrow types commonly found on Assateague Island have been reported for many other species of Ocypode (Vannini, 1980). The burrow served as a protection from predators and conspecifics. The secondary branch of the Y-shaped burrow served as an escape tube or back-door through which the occupant can escape (Cowles, 1908).

During the two years of study, no burrow excavated ever reached the water table nor were two burrows ever found to be connected to each other. Warburg and Shuchman (1979) reported that O. cursor (L.) burrows never reached the water table and Leatherman (1973) stated that no interconnecting burrows were found in O. ceratophthalmus, although burrows reached to or near the ground water level. Teerling (1970), however, reported that O. quadrata burrows on Padre Island, Texas, tended to extend to the water table.

Crabs observed on Assateague Island began construction of a burrow by utilizing their walking legs to test the location before actually starting to dig. Similar behavior has been reported by Hughes (1966) for O. ceratophthalmus. This probing activity could be an effort to determine sand-moisture since Warburg and Shuchman (1979) reported that O. cursor was able to detect and select from alternative substrates having a difference of only 1% moisture.

After an appropriate location had been selected, the crab would make an initial excavation using its walking legs, periodically shift 180 degrees and continue to move sand. When the hole was about one-half the crab's width in depth, the crab used its chela and two adjacent walking legs to carry sand in a fashion similar to that reported for the species by Cowles (1908). Substantially the same mechanisms have been reported for *O. ryderi* (Vannini, 1980), *O. gaudichaudii* (Crane, 1941) and *O. saratan* (Linsenmair, 1967 cited in Vannini 1980).

In both new construction and maintenance activity, sand was brought to the surface and was usually carried some distance from the burrow before being flung with the chela creating a fan-like pattern (Figure 28A). If the crab excavated in moist sand, it formed small sand balls or pellets when the sand was pressed between its walking legs/chela and venter. These sand pellets were often flung causing them to shatter. However, pellets were sometimes dropped or failed to shatter creating a pattern (Figure 28B&C). These observations support statements made by Milne and Milne (1946) for *O. quadrata* (north of Cape May, New Jersey) and those of Coues (1871) for Fort Macon, North Carolina. A third method of disposal was dumping or mound building. In *O. quadrata* the mound was usually constructed immediately adjacent to the burrow (Figure 28D). Hughes (1973) reported that mounds were associated with the burrows of mature males. Similarly, mound-building by *O. quadrata* on Assateague Island was always associated with larger burrows. Letterman (1973), however, reported that no mound building by *O. quadrata* was found on the beach he studied in Delaware.



A

B

Figure 28 Typical sand distribution patterns around O. quadrata burrows; A the fan-like pattern; B the fan-like sand pellet pattern; C another sand pellet pattern; D a typical mound with trampling

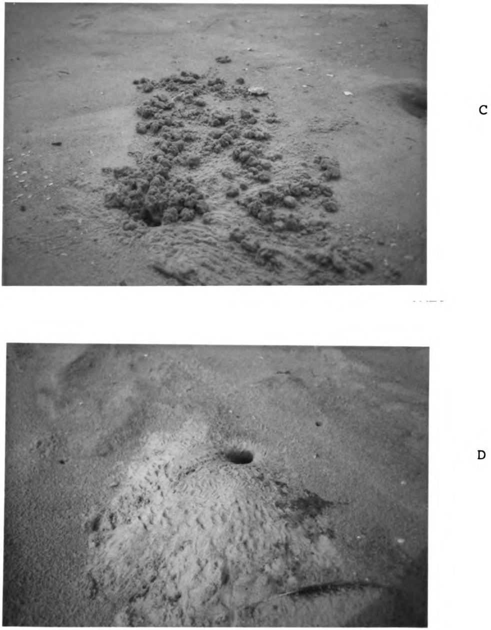


Figure 28 (cont'd.)

Sand brought to the surface by ghost crab burrow construction has the potential to influence the size parameters of beach sediments. Visual observation of excavated sand indicated that it tended to be coarser grained than the existing surface sediments. Although the individual burrow excavations were small compared to the total volume of beach sand, ghost crab activity was continuous and could influence sediment size on Assateague Island. Chakrabarti (1980) reported that sediment reworking by *O. ceratophthalma* on a beach near Gopalpur, India, played an important role in shaping the size parameters of sediments. An investigation of the role of *O. quadrata* burrowing activity on grading beach sediments should prove fruitful. In addition, it could provide additional information on the role and importance of *O. quadrata* in the dynamics of barrier beach ecology.

The crab would usually pause at the burrow entrance prior to entering or exiting during construction and maintenance activities. Similar observations have been reported by Phillips (1940) and Vannini (1980). From time to time during the excavating process, the crab would change sides utilizing the large chela rather than the smaller and visa-versa. This supports Walcott's observations from North Carolina as reported in Vannini (1980). Vannini (1980) suggested that this practice might be used by *O. quadrata* to maintain the symmetry of its burrow. Occasionally crabs were observed flinging sand from within the burrow. Chance and Hobbs (1969) noted a similar behavior for *O. quadrata*.

At times, the crab would pause and trample or pat down the excavated sand. Crane (1941) and Linsenmair (1967, cited in Vannini 1980) stated that this practice renders the presence of the burrow less obvious. This behavior was also observed on Assateague Island in crabs which were constructing mounds. Figure 28D shows a mound on which the sand has been trampled with the chela marks clearly evident. Vannini (1980) reported that trampling might serve to consolidate the surface of the sand pile so that it would resist aeolian transport and prevent the sand from slipping back into the burrow. The crab trampled the sand by utilizing the outer sides of the palm of the chelipeds.

On Assateague Island, the typical burrow opening faced the ocean with the tunnel sloping away toward the dunes at an angle of approximately 45 degrees. Only one exception to this general observation was noted. On October 10, 1981, a number of burrows were aligned parallel to the surf rather than perpendicular to it. In examining the wind direction data (Table 6 Appendix page 170) before and after the period in question, a shift from a generally easterly component to a westerly component was observed. Hill & Hunter (1973) reported a coincidence of burrow orientation and dominant wind direction for _O. quadrata_ on Padre Island, Texas. They suggested that wind direction may be a factor influencing burrow orientation. Chakrabarti (1981), however, reported that for _O. ceratophthalma_ (= _O. ceratophthlmus_) in India, the burrows always were inclined shoreward irrespective of the prevailing wind direction. The seaward orientation of burrows seen for _O. quadrata_ on Assateague was also reported by Cowles (1908) for the Tortougas, Florida, and it correlates well with the information available on other members of the Ocypodidae (Vannini, 1980).

Burrow plugging was frequently observed, especially during mid-day in warmer months. Plugs were constructed in two fashions. The first followed the pattern described by Cowles (1908) where crabs used their walking legs to draw sand into burrows. Pressure was placed on sand from below and the plug was pressed into place usually leaving the crab's leg pattern embossed in its upper surface (Figure 29A). The second method involved pushing up a plug from inside the burrow (Figure 29B). These plugs were usually located deeper in the burrow and their upper surfaces were rough in texture. Plugs served to prevent higher surface temperatures from entering burrows and helped to maintain a more uniform environment within the burrow during short periods of warm weather. Plugging is common within the Family Ocypodidae and has been observed in seven species (Vannini, 1980).

Fellows (1973, cited in Vannini 1980) found moulting *O. ceratophthalmus* and *O. cordimana* and large numbers of ovigerous *O. ceratophthalmus* in long solidly plugged burrows. He assumed that these individuals dug deep burrows which they plugged, and in which they remained until ecdysis was completed or the eggs were ready to hatch. Fellow's theory tends to be supported by Rao (1966) who stated that *Gecarinus* sp. required moist sand, darkness, suitable temperature and privacy to enter proecdysis. Rao also reported that larger *O. macrocera* required privacy for survival and growth and that if moulting took place in the presence of another large crab, the freshly moulted crab was devoured. A burrow could provide all the requirements noted above and, thus, should function well as a moulting chamber. If *O. quadrata* acted in a similar fashion, by constructing deep burrows as suggested by Cowles (1908), this could explain the low number of female crabs found at various times of the year. Burrows

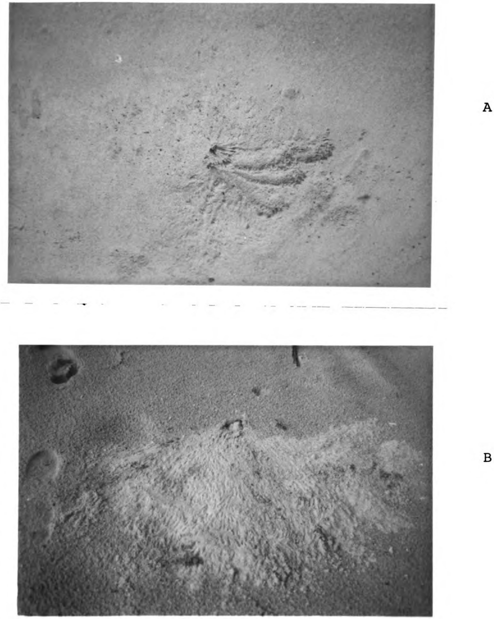


Figure 29 Typical burrow plugs made by *O. quadrata*; A a sand plug with leg prints; B the rough surface plug pushed up from below

plugged from the inside may serve as maternal and moulting chambers, and those plugged at the surface may function to maintain short term optimal moisture and temperature conditions.

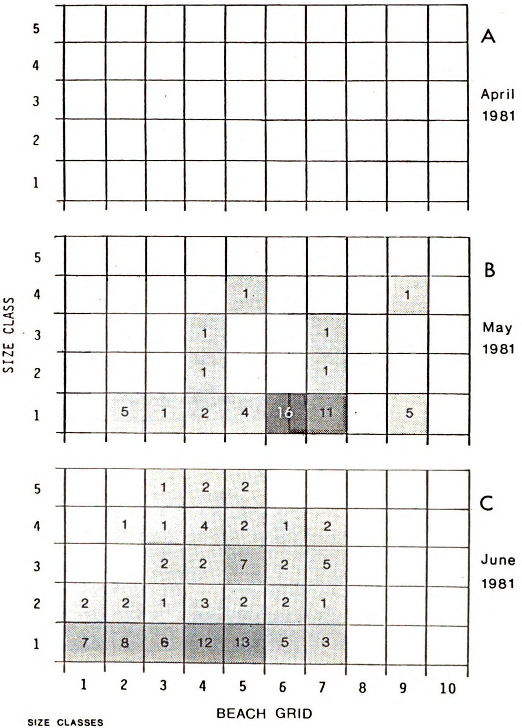
Should *O. quadrata* females remain within a burrow until their eggs were ready to hatch, a new explanation for the behavior of female crabs in the water as reported by Milne and Milne (1946) would be required. Rather than aerating the eggs, as proposed by Milne and Milne, these females could, in fact, be releasing their larvae into the water. Although insufficient data were obtained to prove this theory, the land crabs, *Cardisoma guanhumi* (Latreille), (Stephens, 1965) and, *Gecarcinus lateralis* (Freminville), (Wolcott & Wolcott, 1982) have been reported to vigorously fan their abdomens and vibrate their bodies to release their hatching eggs in the sea.

Observations made during this study indicate that burrow construction techniques utilized by *O. quadrata* on Assateague Island were substantially similar to those used by southern populations. Shape, sand disposal and location/direction on the beach were all similar. The only apparent difference noted was the relationship of burrow depth to the ground water level. *O. quadrata* on Assateague Island were never observed to extend their burrows to the water table, however, the Texas population (Teerling, 1970) tended to extend to the water table.

Distribution on the Beach

O. quadrata on Assateague Island exhibited seasonal differences in distribution. During April when ghost crabs first became active, the population was primarily located behind the dunes with some crab burrows located on the dune's face. All size classes of crabs were

Figure 30 Total number of crabs (recorded as burrows) in each size class by beach grid (1 nearest ocean) for each month in 1981 at transect 1.



A April 1981

SIZE CLASS	1	2	3	4	5	6	7	8	9	10
5										
4										
3										
2										
1										

B May 1981

SIZE CLASS	1	2	3	4	5	6	7	8	9	10
5										
4					1				1	
3				1			1			
2				1			1			
1		5	1	2	4	16	11		5	

C June 1981

SIZE CLASS	1	2	3	4	5	6	7	8	9	10
5			1	2	2					
4		1	1	4	2	1	2			
3			2	2	7	2	5			
2	2	2	1	3	2	2	1			
1	7	8	6	12	13	5	3			

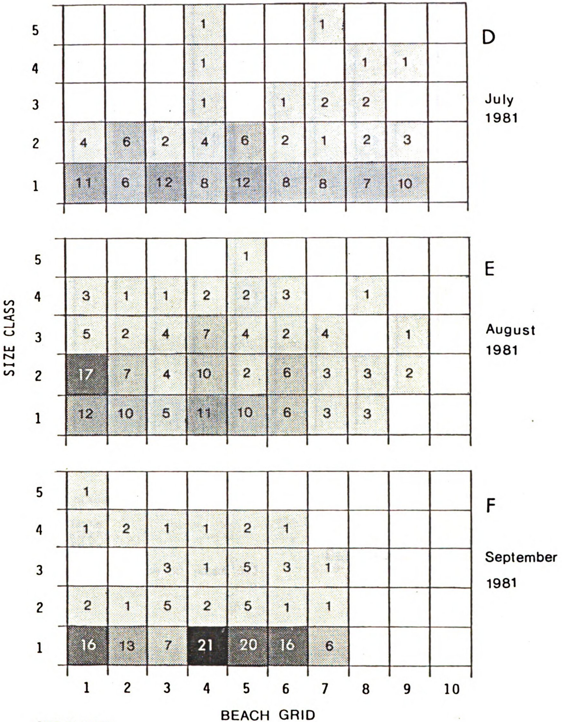
BEACH GRID

SIZE CLASSES
(cm)
1 - 0.1 to 1.5
2 - 1.6 to 2.5
3 - 2.6 to 3.5
4 - 3.6 to 4.5
5 - > 4.5

Relative no. of burrows per grid

░	▒	▒	▓	█
0-5	6-10	11-15	16-20	>20

Figure 30



D — July 1981

Size class	1	2	3	4	5	6	7	8	9	10
5				1			1			
4				1				1	1	
3				1		1	2	2		
2	4	6	2	4	6	2	1	2	3	
1	11	6	12	8	12	8	8	7	10	

E — August 1981

Size class	1	2	3	4	5	6	7	8	9	10
5					1					
4	3	1	1	2	2	3		1		
3	5	2	4	7	4	2	4		1	
2	17	7	4	10	2	6	3	3	2	
1	12	10	5	11	10	6	3	3		

F — September 1981

Size class	1	2	3	4	5	6	7	8	9	10
5	1									
4	1	2	1	1	2	1				
3			3	1	5	3	1			
2	2	1	5	2	5	1	1			
1	16	13	7	21	20	16	6			

SIZE CLASSES
(cm)
1 - 0.1 to 1.5
2 - 1.6 to 2.5
3 - 2.6 to 3.5
4 - 3.6 to 4.5
5 - > 4.5

Relative no. of burrows per grid

0-5	6-10	11-15	16-20	>20

Figure 30 (cont'd.)

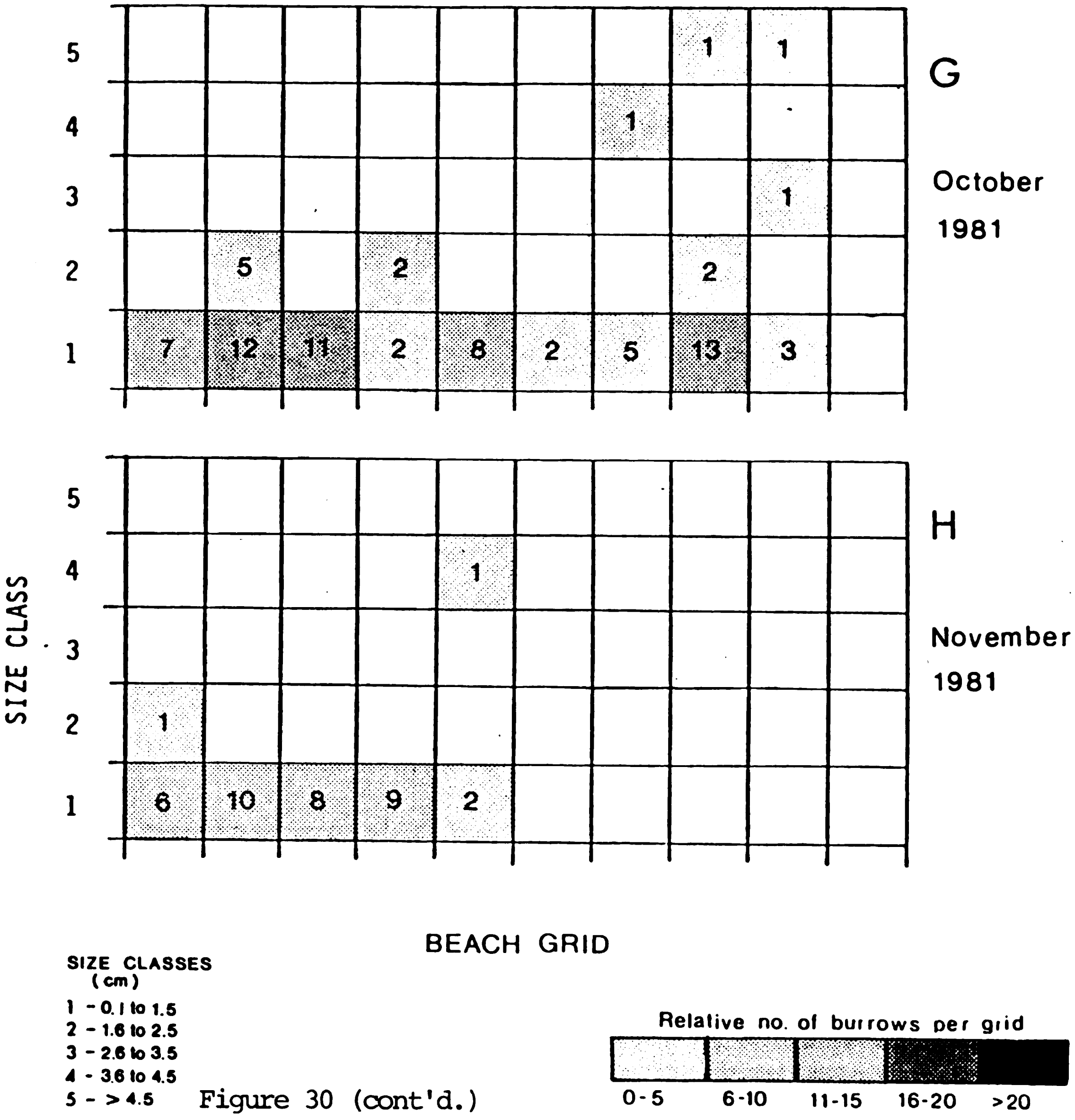


Figure 30 (cont'd.)

Figure 31 Total number of crabs (recorded as burrows) in each size class by beach grid (1 nearest ocean) for each month in 1982 at transect 1.

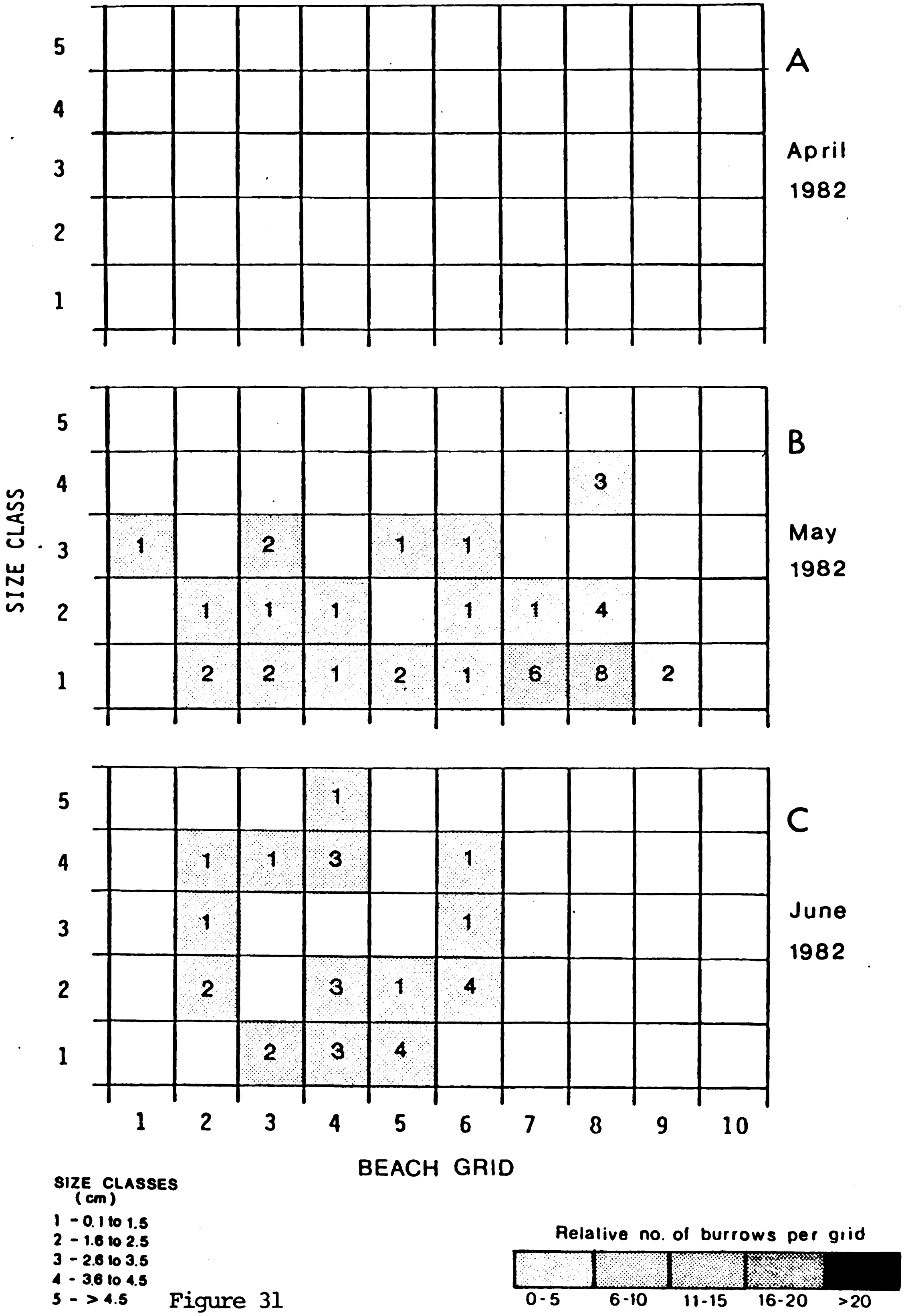
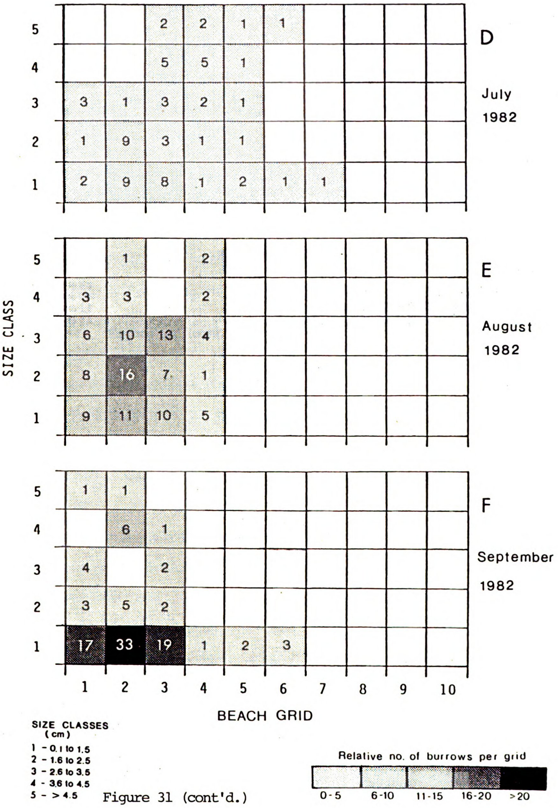

A
April
1982
B
May
1982
C
June
1982
SIZE CLASS
5
4
3
2
1
3
1 2 1 1
1 1 1 1 1 4
2 2 1 2 1 6 8 2
1
1 1 3 1
1 1
2 3 1 4
2 3 4
1 2 3 4 5 6 7 8 9 10
BEACH GRID
SIZE CLASSES (cm)
1 - 0.1 to 1.5
2 - 1.6 to 2.5
3 - 2.6 to 3.5
4 - 3.6 to 4.5
5 - > 4.5
Relative no. of burrows per grid
0-5
6-10
11-15
16-20
>20

Figure 31



D July 1982

SIZE CLASS	1	2	3	4	5	6	7	8	9	10
5			2	2	1	1				
4			5	5	1					
3	3	1	3	2	1					
2	1	9	3	1	1					
1	2	9	8	1	2	1	1			

E August 1982

SIZE CLASS	1	2	3	4	5	6	7	8	9	10
5		1		2						
4	3	3		2						
3	6	10	13	4						
2	8	16	7	1						
1	9	11	10	5						

F September 1982

SIZE CLASS	1	2	3	4	5	6	7	8	9	10
5	1	1								
4		6	1							
3	4		2							
2	3	5	2							
1	17	33	19	1	2	3				

Figure 31 (cont'd.)

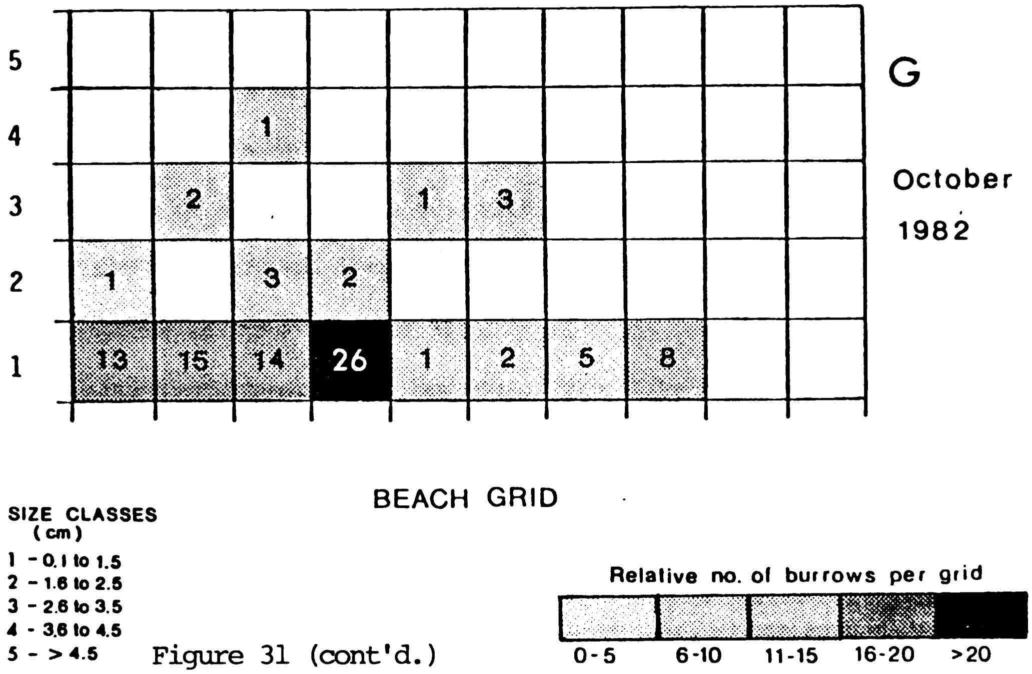


Figure 31 (cont'd.)

found in the area behind the dunes in 1981 and 1982.

Larger burrows tended to be concentrated toward the dunes following emergence of O. quadrata on the beach in May of both years. Burrows in size class 1 (0.1-1.5 cm) were located across most of the backshore, although they still had a greater concentration toward the dunes (Figures 30 and 31).

The densest aggregation of burrows, from July through September 1981, was in or adjacent to grids 4 and 5 with the larger burrows still remaining closer to the dunes. Burrows in size class 1 (0.1-1.5 cm) still remained fairly evenly distributed across the backshore (Figure 30). In 1982, from July through September, ghost crabs were located closer to the seashore with maximum population aggregations in grids two and three (Figure 31).

Direction of migration was reversed in the fall of 1981 and 1982. Figure 30G&F for 1981 showed this trend. This was particularly evident in the larger crabs (only 5 grids were in the sample in November, 1981). While the area behind the dunes was not part of the regular sampling program, visual observations confirmed the use of this area by ghost crabs.

Although the majority of burrows were located behind the crest of the berm on the backshore, burrows were observed in the intertidal foreshore on several occasions. Burrows on the foreshore were not included in the study results since each survey was begun at the upper limit of the previous high tide close to the berm (see page 20).

Juvenile O. quadrata (size classes 1 and 2) were more evenly distributed on the backshore than previously reported in the literature (Milne & Milne, 1946; Fisher & Tevesz, 1979). Juvenile distribution/abundance was not tied to the high water line or in close proximity to the sea as reported for *O. cursor* (Warburg and Shuchman, 1979). In addition, maximum densities did not occur immediately behind the berm as reported by Hedgpeth (1957) for *Ocypode*, but rather 12 to 8 m from the berm in 1981 and 1982 respectively.

Weather events (storms) also influenced the distribution of *O. quadrata*. In 1981 and 1982 storms occurring along the coast resulted in an increase in *O. quadrata* activity in the area behind the dunes and crowded the burrows remaining on the beach into the area close to the dunes. On several occasions this displacement was 100 m or more behind the dunes. Burrow activity behind the dunes, both as a result of migratory movements and storm events, was usually associated with areas where vegetation occurred. Teerling (1970) reported a similar relationship for *O. quadrata* burrows behind the dunes on Padre Island, Texas.

O. quadrata may migrate behind the dunes in the fall to improve its ability to successfully overwinter. Burrows constructed behind the dunes would be protected from damage during the severe winter storms which occur along the northeast coast. Burrows on the backshore, however, would be subject to destruction as storm-induced waves shift the beach profile. The destruction of burrows in this manner was observed several times during the study. The dune face itself, on one occasion, was eroded and burrow openings were exposed. Because *O. quadrata* cannot tolerate low temperatures (12°C), exposure of this type during winter would most likely result in death.

Data collected during this study was insufficient for an evaluation of differences in burrow locations between males and females. However, Vannini (1980) reported that *O. ryderi* on the beaches of Sar Uanle, Somalia, displayed a variation of burrow locations with males and juveniles burrowing lower on the beach and females burrowing on the dunes. Fellows (1975) stated that male *O. laevis*, in Hawaii, burrowed in the uppermost intertidal and dry beach zone and mature females and juveniles inhabited the strand vegetation just inland of the beach.

Burrows of *O. quadrata* on Assateague Island generally occurred in the same area of the beach as populations to the south. Juveniles tended to be more evenly distributed on the beach than previously reported for populations to the north and south. There was a correlation between increased burrow activity behind the dunes and storm events for both the Assateague Island population and the Padre Island, Texas, population.

Activity Period

Yearly:

Crabs on Assateague Island became active during mid-to-late April. Activity began in the vegetated areas behind the dunes and on the upper section of the backshore. The air temperature at this time of the year (based on the monthly average air temperature, Table 1, (Appendix page 166) was 12.2°C. Temperatures measured at Ocean City, Maryland in Tables 6 and 7 (Appendix pages 170 & 171), show April 17, 1981, 17.2°C and April 13, 1982, 9.4°C. A number of intact dead ghost crabs were found on the surface near transect 1 during this mid-April period in 1982 . Temperatures at night during this period ranged from -1.1°C to 4.4°C. Possibly, these crabs emerged early and were unable to survive the cold temperatures. Leggett and Butler (1975) reported a similar event for their survey site near Virginia Beach, Virginia, and Milne and Milne (1946) reported that O. quadrata died quickly when placed in a refrigerator at 12°C.

Crabs became active on the beach, and counts were begun during the first week of May in both 1981 and 1982. The Ocean City, Maryland temperature was 15°C on May 3, 1981 and on May 7, 1982. This temperature compares favorably with the 16°C reported by Haley (1972) for the onset of O. quadrata activity in Texas. Onset of activity in May also correlates favorably with Wolcott's (1978) report on O. quadrata activity at Fort Macon, North Carolina, in which he stated that activity began in late May.

Over-all activity increased in June and July, peaked in August in both 1981 and 1982, and declined through October in 1982 and November in 1981. The monthly average air temperature for this period (Table 1, Appendix page 166) was 15°C in October and 8.4°C in November, while the Ocean City, Maryland, temperatures recorded for the sample dates were 15.6°C for November 11, 1981, and 10°C for October 29, 1982. Again, there was good agreement with Haley's (1972) 16°C activity threshold and Wolcott's (1978) finding of no significant activity at Fort Macon, North Carolina, after November. Thus, O. quadrata activity in both northern and southern populations appeared to be closely correlated with temperature.

Daily:

Ghost crabs on Assateague Island were active diurnally and nocturnally with the major activity period occurring from approximately dusk to 0800 hours the next morning. This time frame compares favorably with Wolcott's (1978) observations for O. quadrata in North Carolina and de L. Brooke's (1981) report on *O. ceratophthalmus* on Cousin Island, Seychelles. Haley (1969) and Hill and Hunter (1973) reported a similar pattern for *O. quadrata* on the Barrier Islands along the Texas coast. Crane (1941) reported that *O. occidentalis*, an analogous species to *O. quadrata* on the western coast of the America's, were nocturnally active as adults.

Crane (1941) and Hughes (1966) reported that the activity patterns of adults and juveniles were different. They stated that this might be a measure used to avoid predation by adult conspecifics. Hughes (1966) speculated further that the predominantly diurnal activity by juveniles could be related to their relatively limited visual capabilities, rendering them less aware of potential predators and other factors (such as man).

On Assateague Island crabs were usually active at transect 1 during the entire day, although the major activity period was from early afternoon until about dawn the following day.

Although crabs were active all day, the casual observer walking on the beach would not notice any significant activity as the crabs quickly detected intruders and darted into their burrows. Hughes (1966) reported that *O. ceratophthalmus* adults were able to perceive moving objects at great distances (>100 m) and were therefore difficult to observe. If disturbed, crabs on Assateague Island returned to their burrows or vanished in the surf. If an observer remained still at any location for a period of time, the crabs would re-emerged and resume their normal activity. When observed in this fashion, crabs were not inhibited and would follow their normal routine.

Burrow maintenance, followed by wandering, was the primary occupation engaged in by crabs during the minor activity periods (dawn to 1200 hours and 1600 hours to dusk). Wandering consisted of moving across the surface of the backshore, in a random fashion. Few if any crabs, except those with burrows, were active on the foreshore. Crabs frequently engage in agonistic behavior while wandering. An additional activity that was observed during this time period involved the "testing" of sand with the chela. This behavior involved the wandering crab moving about the backshore with its chela held out and pointed down. Periodically the crab stopped and moved the chela to the mouth parts in a fashion similar to deposit feeding. While the crab undoubtedly picked up and ingested sand, it was not possible to observe what was actually being moved to the mouth. This activity never lasted very long, and upon completion the crab resumed wandering. Crabs also investigated objects on the beach during short forays from their burrows. If the object was edible it was fed upon in place or dragged back to the burrow. Haley (1969) and Wolcott (1978) both reported similar diurnal activity for O. quadrata, although from their accounts, this activity appeared to be more prevelant on Assateague Island, Maryland, than at their study sites in Texas and North Carolina respectively. Wolcott (1978) specifically mentioned that crabs made short forays to investigate objects on the beach and subsequently fed on edible items.

Crabs began to plug their burrows about 12 noon. Burrows which were plugged generally remain so until around 1600 hours when the second minor activity period usually began. After emerging from their burrows around 1600 hours, ghost crabs on Assateague Island engaged in burrow maintenance and wandering, a pattern similar to their behavior for the period from 0800 to 1200 hours. As evening progresses, more crabs became active and at about sunset, or shortly thereafter, the majority of the population was on the beach. The primary activity engaged in during the night was related to feeding. Crabs moved from the backshore to the foreshore where they foraged along the water's edge until dawn when they returned to the backshore. This pattern of activity was repeated consistently from May through September in both 1981 and 1982. Similar patterns have been reported for _O. quadrata_ by Hill and Hunter (1973) and Wolcott (1978), although Wolcott reported that crabs went directly to the water upon emerging from their burrows at dusk, rather than engaging in a period of burrow maintenance and wandering. Crane (1941) reported a delay of approximately one hour, following emergence from their burrows, before _O. gaudchaudii_ moved toward the edge of tide to feed. In October and November, however, crab activity near the water's edge appeared to be reduced. During this period crabs tended to remain on the backshore in close proximity to their burrows.

Normal daily activity patterns can be disrupted by weather events or human activity. Blowing sand, temperature, heavy rain, and human activity were observed to lessen or eliminate ghost crab activity on Assateague Island. Teerling (1970) reported that _O. quadrata_ activity was depressed by winds greater than 10 knots or rainfall in excess of 25 mm for a single event. Wolcott (1978) stated that strong onshore winds obliterated burrows in the foreshore and forced the crabs inland to burrows in the lee of dunes or vegetation. Hughes(1966) noted that no _O. ceratophthalmus_ emerged following a rain shower at 2030 hours.

He also reported that activity was reduced or absent on windy days when sand was blowing at ground level. Hughes also reported that a sudden cold spell, which dropped the air temperature to 12.4°C, resulted in a nocturnally active population becoming inactive for two weeks. Normal activity on this beach did not resume until the temperature reached 16°C. Crabs normally diurnally active, however, remained active during the cold spell.

Human use, as stated previously, also reduced crab activity. Hikers, picnickers or other human users of the beach prevented the crabs from engaging in their normal routine. Interruption may force the crabs to become more nocturnal or to conduct their activities within a shorter time period. Hughes (1966) stated that the degree of diurnal activity above sand for _O. ceratophthalmus_ on Inhaca Island, Mocambique, was related to the amount of human activity on a particular beach. He noted that _Ocypode_ populations on virtually uninhabited islands or infrequently used beaches were active diurnally and nocturnally, but that those on beaches with heavy human use were solely nocturnal. Occasionally frequented beaches showed intermediate degrees of activity.

On Assateague Island, transect 1 was infrequently used while transects 2 and 3, although receiving different types of use, were heavily utilized respectively. As a result, crabs at transect 1 were both diurnally and nocturnally active while crabs at transect 2 and 3 were primarily nocturnal.

Based on a comparison of the findings of this study with daily activity patterns reported in the literature, _O. quadrata_ behaves in a similar fashion along its range on the East and Gulf coasts.

O. quadrata on Assateague appeared to be slightly more diurnally active than populations to the south. In addition, crabs engaged in a period of wandering and burrow maintenance on Assateague Island before moving to the fore shore to feed rather than moving immediately to the beach to feed as reported for a population in North Carolina. Weather impacted activity patterns in a similar fashion on Assateague and to the south.

Food/Feeding

O. Quadrata, on Assateague Island was primarily a predator, feeding principally on the mole crab, E. talpoida. They were omnivorous faculative scavengers as well, feeding on virtually any food source available. This observation conflicts with the earlier accounts of Cowles (1908), Phillips (1940) and Teerling (1970) who reported that O. quadrata was primarily a scavenger, but supports the findings of Milne and Milne (1946), Letterman (1973) and Wolcott (1978) who reported on the feeding patterns of O. quadrata in New Jersey, Delaware and North Carolina respectively.

Milne and Milne (1946) stated that O. quadrata in New Jersey captured small beached fish along the line of beach drift or close to the limit of wave advance, if the tide was high. They also noted that O. quadrata would accept insects (dead or alive, dry or fresh) or other animal matter from a pair of forceps. Mole crabs were eagerly accepted by hungry crabs. Letterman (1973) experimented with various foods (fish, insects, mole crabs, amphipods, clams, conspecifics [juveniles], starfish, algae and jellyfish) and concluded that, if given a choice, O. quadrata preferred living organisms. Finally, Wolcott (1978) reported that live prey (mole crabs, E. talpoida and coquina clams, *Donax variabilis* Say) made up more than 90 percent of the diet of *O. quadrata* at Fort Macon, North Carolina.

O. quadrata began to search for food soon after their arrival on the forebeach of Assateague Island. Crabs positioned themselves on the beach along a line at the upper edge of the area overwashed by incoming waves. *O. quadrata* flattened themselves on the beach with their walking legs extended and the outer surfaces of both chela on the sand. Crabs remained motionless with their walking legs usually anchored in the sand for a period of time before moving to a new location. Periodically, crabs in this position began to dig rapidly and then plunged their chelae into the excavation attempting to capture a mole crab. Following the capture of a mole crab, *O. quadrata* left the wave zone and moved to a position near the crest of the berm. They consumed their prey by tearing it apart with their chelae and mouth parts. Similar reports on capture technique have been made by Letterman (1973) and Fales (1976), with Milne and Milne (1946) and Fales (1976) noting analogus methods of feeding.

O. quadrata, in some cases, took its prey back to its burrow where it would consume the organism while sitting on the sand outside the burrow entrance. It was common to find remains of *E. talpoida* adjacent to ghost crab burrows during morning surveys.

Similar feeding methods have been reported by Hughes (1966) for *O. ceratophthalmus* on Inhaca Island on the coast of Mocambique. He reported that *Macrophthalmus grandiderii* M. Edw. were either perceived visually and captured, or detected tactically by using the legs to "test" in shallow puddles. Buried juvenile penaeid prawns were also captured utilizing this same "testing" movement of the legs. Hughes also reported that *O. ceratophthalmus* was adept at locating and capturing *D. faba* Gm. and *D. incarnata* (Gm.). The clams were dug with one or two quick movements of the walking legs and crushed with the chela.

O. quadrata may utilize the tactile hairs on its walking legs to detect various prey species. Letterman (1973) reported a similar method of prey capture. Trott and Robertson (1984), however, demonstrated that *O. quadrata* was able to detect chemical stimulants applied to their chela. They speculated that this ability would be valuable in detecting food, and that certainly tactile and chemical cues would be important to active predators of *D. variabilis* and *E. talpoida*. Since *O. quadrata* searches for *E. talpoida* by positioning the outer surface of its chela on the beach surface, they may be receiving chemical stimulation which could be utilized as a cue to aid in predation.

No crabs were observed to engage in deposit-feeding and resultant formation of pseudofecal pellets. *O. quadrata* moved material to their mouth parts in a fashion similar to deposit-feeding, but no pseudofeces were ever found. Milne and Milne (1946) reported similar findings for their study site in New Jersey. Robertson and Pfeiffer (1982), however, reported that *O. quadrata* fed on macroscopic detritus on a Georgia barrier beach. During their study on a secluded barrier beach on Sapelo Island, Georgia, they stated that *O. quadrata* exhibited deposit-feeding similar to *Uca pugilator* (Bosc) as well as predatory behavior. They reported that *O. quadrata* deposit-fed in a unique manner utilizing the articulating function of the chelipeds. *O. quadichaudii* (Crane, 1941) and *O. ceratophthalnus* (Tweedie, 1950), unlike *O. quadrata*, raked the sand from the substrate without using the articulating function. *O. quadrata* also used the minor chela to remove the feeding pellet from the buccal region. Other species simply allowed the pellets to drop (Crane, 1941; Tweedie, 1950). Robertson and Pfeiffer (1982) reported that *O. quadrata*, although poorly suited for scavenging macroscopic detritus (Wolcott, 1978), were 90 percent as efficient at this activity as *U. pugilator*, which derives its major nutrient intake through deposit-feeding.

Crane (1941) provided one possible explanation for this deposit-feeding behavior. In her report on *O. quadichaudii* and *O. occidentalis*, from the western coast of Central America, she noted that *O. quadichaudii*, which was found on beaches with minimal wave energy (protected) and on the shores of lagoons, was a deposit-feeder but that *O. occidentalis*, which was almost always found on high energy beaches, was a typical predator/scavenger.

O. quadrata deposit-feeding observed by Robertson and Pfeiffer (1982) occurred on both a protected and exposed sandy beach which contained dense patches of psammophilic algae. However, even the exposed beach was subjected to limited wave energy (breaker heights average only 20 cm). This situation appears to be analogous to the conditions reported by Crane (1941) for *O. quadichaudii*. Beaches at Assateague Island, Maryland and Fort Macon, North Carolina, are exposed to considerably greater wave energy. Thus, there never was any apparent accumulation of psammophilic algae.

Deposit-feeding may be an important feeding behavior for *O. quadrata* in certain sections of its range but this feeding mode plays a minor role where high quality prey was available, especially near the northern limits of its range. *O. quadrata*, however, appeared to be a facultative feeder with its feeding behavior determined by the availability of various food items. In areas where *Emerita* sp. and *Donax* sp. were available, they appeared to be the food of choice. In other locations where these species were not as plentiful, scavenging and perhaps deposit-feeding played a greater role in *O. quadrata* nutrition. This appeared to be the case in Bermuda and along the Texas coast (L. Powers, Pers. Comm., in Wolcott, 1978) and might also explain Cowles' (1908) observations on Loggerhead Key, Florida and Teerlings' (1970) observations along the Texas coast. Powers, however, noted that much of the apparent scavenging (picking over material along the drift line) was actually predation. *O. quadrata* frequently captured *Portunus sayi* (Gibbes), a small crab associated with the *Sargassum* sp. stranded on the shore. This information correlates with Letterman's (1973) observations that crabs picking over beached algae might actually have been feeding on numerous small amphipods found in and on the algal mass. Thus, even while appearing to scavenge, *O. quadrata* may often be a predator.

O. quadrata also commonly fed upon a wide variety of other foods including hatchling turtles, lizards, land crabs, hermit crabs, fiddler crabs and insects. Phillips et al (1969) reported that *O. quadrata* would feed on, and drag to their burrow entrance, stranded Portuguese men-o-war *Physalia physalia*. McLachlan (1980) stated that *O. ryderi*, on the southeastern coast of South Africa, also fed on *Physalia* sp., although, they pulled the stranded organism into their burrows. On Assateague Island, *O. quadrata* was observed feeding on amphipods, beached fish and insects, as well as mole crabs.

On Assateague Island, O. quadrata was observed dragging food into its burrow. On several occasions during the two years of the study, trials were conducted on the beach in the evening to investigate the reaction of O. quadrata to inanimate objects (some food, some not). These items consisted of meat, cheese, apple cores, cherry pits and mole crabs which were thrown from a stationary four-wheel drive vehicle so that they landed in the proximity of a crab that was active on the surface. In almost every case the crab rushed to the item and carried it back to its burrow. In several trials the crab fed on the item in place, especially if the item was large. Some crabs carried more than one item down their burrow and one small crab carried three pieces of cheese down its burrow. This could be a long-term food conservation technique or a short-term mechanism to protect food from other crabs. However, no food items were ever noted in any of the burrow casts.

These trials indicated that O. quadrata was visually stimulated by movement, which was most likely construed as prey. Letterman (1973) reported a similar result for O. ceratophthalmus and Cowles (1908) reported that O. quadrata on Loggerhead Key, Florida exhibited the same behavior.

Cannibalism was observed in O. quadrata on Assateague Island, Maryland, and Cowles (1908) reported that O. quadrata was cannibalistic on Loggerhead Key, Florida. However, neither population appeared to be as cannibalistic as O. ceratophthalmus (Hughes, 1966; Letterman, 1973).

O. quadrata on Assateague Island, captured live prey (mole crabs and coquina clams) in a similar fashion to the population located in

North Carolina. In these locations live prey provided the majority of the crabs energy requirements. In populations in Texas, scavenging appeared to provide a greater portion of *O. quadrata's* needs although they might actually be capturing live prey associated with the drift material. Deposit-feeding did not appear to provide a significant portion of the crabs needs except possibly in Georgia. *O. quadrata* feeding patterns were similar among the various populations utilizing the same or similar prey/food source. Their feeding habits were, however, quite variable changing to suit the locally or seasonally abundant food source.

Predators

Predation on *O. quadrata* was not observed during the two years of this study. In August of 1980, however, during one of the trips made to Assateague Island in preparation for the study, indirect evidence of predation by the red fox, *Vulpes fulva* (Desmarest), on *O. quadrata* was obtained. This evidence consisted of 15 randomly spaced digs along a section of beach approximately 2.5 km long, north of transect 1. The digs were similar to holes dugs by dogs. They were narrower at the bottom, widening as they reached the top and usually oval at the surface. The digs were approximately 13-18 cm in width, 31 cm in length and 31-46 cm in depth. The excavated material was cast adjacent to the hole in either a single or double pile. The sand piles were approximately 20 cm in height, 31-39 cm in width, and 46-60 cm in length. Figure 32 shows two views of a typical dig.

The continuation of the crab's burrow was seen at the bottom of several of the excavations. Various remnants of *O. quadrata* were observed in two digs. These consisted of a large chela at one dig

Figure 32 Two views of a typical dig showing the shape of the hole and the sand pile. Note the paw print near the center of the sand pile in the upper photograph.

and, at the second dig, a portion of the ventral section of a carapace with two walking legs attached. Similar digs were observed, along with fox tracks, on several occasions in 1981 and 1982. In addition, red fox were observed on the beach during several night patrols with park rangers. Finally, *O. quadrata* remains were common in fox scat on Assateague Island (Al Wesche, personal communication). Based on this evidence, the red fox probably preys upon *O. quadrata* on Assateague Island and thus, utilizes the energy transported landward from the filter feeding surf-zone populations by ghost crabs.

Various authors have reported vertebrate predation on *O. quadrata* and on other species of the genus. Teerling (1970) reported that coyotes, *Canis latrans* Say, and laughing gulls, *Larus atricilla* Bruch, were predators of *O. quadrata* on Padre Island, Texas. McLachlan (1980) stated that *O. ryderi* was preyed upon by the Cape Gray mongoose, *Myonax pulverulentius* (Wagner), and the yellow mongoose, *Cynictis pencillata* (G. Cuvier), which dug them out of their shallow burrows. At Sar Uanle, Somalia, Messeri (1978, cited in Vannini 1980) reported that baboons, *Papio cynocephalus* L., were observed digging out *O. ryderi* with their hands and some times used cuttlefish bones as tools. Alexander (1979) reported that on Aldabra, Seychelles, *O. ceratophthalma* was fed upon by short-line turnstones, *Arenaria interpres* (Linnaeus) and crab plovers, *Dromas ardeola* Paykull. Further inland, *O. cordimana* was fed upon by pied crows, *Corvus alba* Muller. Vader (1982) reported that pied wagtails, *Motacilla aguimp* Dumont, fed on young *Ocypode* spp. on the beach at Watamu, Kenya.

Based on the results of observations conducted during 32 sampling periods on Assateague Island, *O. quadrata* usually avoided predation by seeking refuge in its burrow or one that belonged to a neighbor. Caught away from its burrow and unable to seek refuge in another burrow, ghost crabs fled down the beach or entered the ocean. When closely pursued, crabs lifted the fourth pair of walking legs and ran on the other six. This behavior was also reported for *O. quadrata* by Milne and Milne (1946) and Letterman (1973).

Some crabs, when unable to find a burrow, ran until they reached a shallow depression or foot print in the sand. Upon reaching the depression, they immediately dropped into it and rocked backwards pushing the posterior portion of the carapace into the sand. During this movement the fourth pair of walking legs were used to throw sand over the dorsal surface of the carapace. Upon completion of this action the crab was virtually buried with only the eyestalks remaining above the surface of the sand. Crabs remained in this position until danger had passed and then re-emerged and continued their activity. Cowles (1908), Milne and Milne (1946) and Letterman (1973) reported similar behavior for *O. quadrata*.

O. quadrata on Assateague Island, Maryland and Padre Island, Texas, were preyed upon by vertebrates although the predators differed between locations. Predator avoidance consisted of seeking refuge in their burrows or that of a neighbor entering the ocean or burying themselves in the sand, and was similar in both northern and southern populations. Thus, these aspects of *O. quadrata's* ecology appeared to be similar in both northern and southern populations.

Human Use Impacts

O. Quadrata abundance (recorded as numbers of burrows) was monitored at three locations on a bi-weekly basis during the two years of this study. Each study site was located in a zone on the beach that received a different type of human use. Transect 1 was located in Zone 1 and received only minor human interference. It was a secluded beach and was used as the experimental control (Figure 33A). Transect 2 was located in Zone 2 and received moderate use from campers in the adjacent North Beach Campground, and some official vehicle traffic (Figure 33B). Transect 3 was located in Zone 3 and received heavy use from off-road recreational vehicles (ORV) and a level and type of human use similar to transect 2 (Figure 33C&D). Recreational use in Zone 3 declined southward to the Maryland/Virginia state line, a distance of 22.5 km from Dune Crossing No. 1. Transect 3 was located approximately 1.6 km south of the entrance to Zone 3 (Dune Crossing No. 1).

The abundance of O. quadrata at transect 1 followed a pattern similar to the graphs depicting growth (pages 95 and 96), with peaks corresponding to the arrival of recruits Figures 34&35 (data in Tables 16-21 Appendix page 184). Although this location received human use (approximately 90 percent walking, Figure 17C&F) it was very limited. An average of one to four individuals an hour walked past the experimental site. Most of these individuals walked on the hard packed sand of the foreshore and, thus, had a minimal impact on the abundance of O. quadrata which were concentrated above the berm crest.

The abundance of O. quadrata at transect 2 was lower than transect 1 in 1981 and 1982 (P=.01 and .05 in 1981 and 1982 respectively). Comparisons of mean burrow diameter between transect 1 and transect 2 showed a statistically significant (P=.01) difference in 1981, but no significant difference (P=.20) in 1982 (Figures

A

B

Figure 33 Typical beach conditions and activities at all three experimental locations; A transect 1; B transect 2; C & D transect 3 in the ORV zone.

C

D

Figure 33 (cont'd.)

ecosystems. Once begun, the degradation it produced in the complexities of physical and biological inter-relationships were rapid. Trew (1973) observed that trampling exerted a direct suppressional force upon a vegetation sere, restricting colonization by more complex species. Trampling affected and altered the physical constituents of the ecosystem as well, by breaking up the top layer of the sandy soil but compacting it slightly at depth. However, Trew (1973) reported that vegetative removal brought about serious changes in physical parameters in sandy regions since, erosion by natural processes became rapid. Liddle and Greig-Smith (1975) reported that trampling reduced both species number and diversity and suggested that the ecological consequences of wear by vehicles and human trampling at their study site (Aberffraw sand dunes, Anglesey, North Wales) were as great as the major natural environmental factor (soil water content).

Vegetation behind the dunes was not adversely impacted by human use at either transect 1 or 3 (Figure 36A&C) and crabs were observed behind the dunes at transect 1 on numerous occasions, especially following storm events. Ghost crabs were rarely observed behind the dunes at transect 3 and infrequently observed in this zone at transect 2 (Figure 36B). Finally, the density of ghost crabs could be impacted by the limited official vehicle use that occurs in this area.

It appears that one or more of these factors were responsible for the shift in density observed at transect 2. Two of the possible causes were a direct result of the camping which takes place adjacent to this site. It appears that direct impacts from individual human uses (excluding official vehicle traffic) were responsible for the depressed densities of *O. quadrata* at this location.

The kind of human use that actually resulted in depressed levels of abundance at transect 2 could be of several types. The first, as noted previously, was that increased human use reduced crab activity. The beach at transect 2 was lightly to moderately used (0.5 to 1.0 individuals per meter of beach per day respectively) beginning shortly after 0600 hours and extending to around 2200 hours. The maximum use, however, was from around 1000 hours to 1600 hours which coincided with the crab's minimum activity period at transect 1. Human uses that occurred during the morning and evening periods could have had a significant impact on burrow maintenance, wandering and feeding activities.

A second possible mechanism for this observed impact could be the human use of the backdune zone and subsequent reduction of vegetation in this zone. Fisher and Tevesz (1979) reported that active burrows were never observed in largely unvegetated back dune areas. Teerling (1970) reported that the vegetational condition of the backdune played an important role in maintaining crab densities (noted as burrows) on the forebeach (backshore and foreshore zones). She stated that the amount of vegetation in the backdunes influenced the density of burrows on the forebeach. In zones where human use had reduced vegetation, fewer burrows were found on the forebeach than in similar areas where vegetation was not so impacted. Crabs used this vegetated zone as a refuge and their numbers increased behind the dunes as they decreased on the forebeach.

Although one might assume that human trampling would have minimal impacts of dune/beach vegetation, such is not the case. Trew (1973) reported that trampling was a powerful force of alteration in all

An analysis of the types of human uses reported by Steiner and Leatherman (1981) and those reported in this study clarify the differences in crab feeding behavior. In the northern site (transect 2) human use came predominantly from campers located in the adjacent campground. These individuals had fixed campsites behind the dunes, and tended to return to this location for their meals. They generally did not carry food to the beach and consequently, little refuse was left behind to attract ghost crabs. At the southern site (Toms Cove, Virginia), studied by Steiner and Leatherman (1981), human use of the beach was day use only (no camping). Visitors to this beach parked in a nearby lot and carried their supplies to the beach. This type of user most likely carried a lunch and probably left food scraps on the beach. Thus, at the northern location (transect 2), there was little or no additional source of food to offset the impacts of human use on the population of _O. quadrata_, while at the southern end of Assateague Island (Toms Cove, Virginia) food scraps left behind by beach users readily attracted ghost crabs.

As noted previously (Activity Section, page 122) human use of the beach results in reduced diurnal crab activity (Hughes, 1966). This type of impact could be responsible for the depressed population level of _O. quadrata_ at transect 2. This population had fewer individuals than the population at transect 1, although size class structure was similar at both locations. The populations differed only in their relative abundance. The physical features of the locations were similar. There was no difference in the availability of their major prey species (_E. talpoida_). Therefore, human use was the apparent causative factor responsible for the reduced abundance at transect 2.

34B&35B). A comparison of mean burrow depth found no significant difference (P=.20) between these two locations in either year (Figures 34A&35A). A final comparison between transect 1 and 2 was made utilizing the size class distributions recorded for these two locations. This evaluation showed no statistically significant difference (P=.01) between these two sites except for one sampling period on June 5, 1981.

The burrows at transect 2, on June 5, 1981, were primarily in the first two size classes (0.1-1.5, 1.6-2.5 cm) and those at transect 1 mostly within the first four size classes (0.1-1.5, 1-6-2.5, 2.6-3.5, 3.6-4.5 cm). The abundance of ghost crabs was reduced at transect 2, but the size class distribution was similar to transect 1 (control).

These results conflict with those published by Steiner and Leatherman (1981) with respect to the effect of human use (beach uses, e.g., sunbathing, picnicking, swimming) on crab density. During this study a significant difference in the density of ghost crabs was recorded (based on burrow counts) between transect 1 (control) and transect 2 (beach use). Steiner and Leatherman (1981), however, reported that the density of ghost crabs on the swimming beach (Toms Cove, Virginia, on the southern end of Assateague Island) was significantly greater than that of the natural beach (refuge beach north of the swimming beach). They speculated that crabs aggregated in this location to feed on scraps of food left by human beach users. Both Cowles (1908) and Teerling (1970) reported that _O. quadrata_ tended to concentrate around locations where scraps of food would be available. This behavior was not observed during the two years of this study on the Maryland portion of Assateague Island.

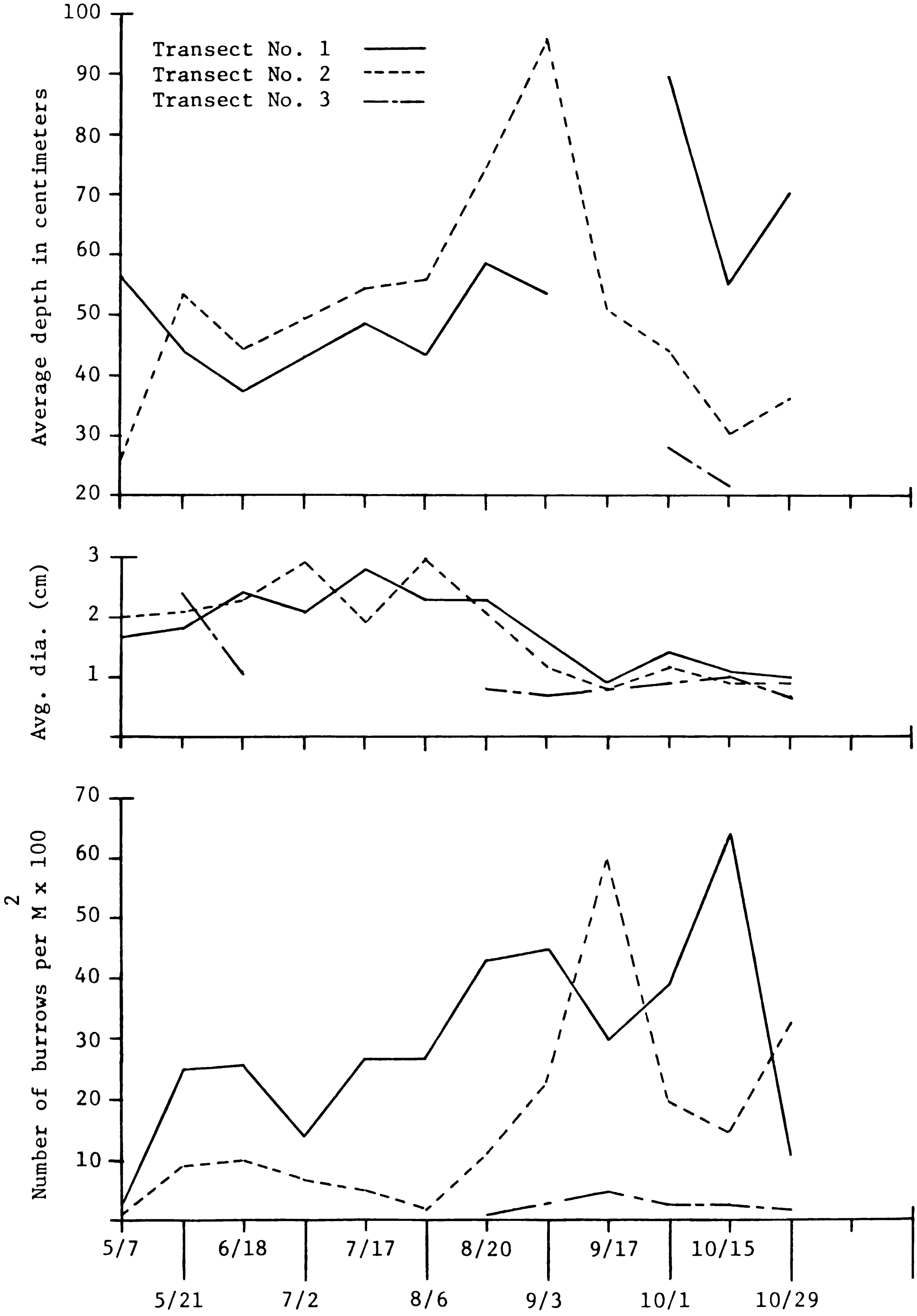

Transect No. 1
Transect No. 2
Transect No. 3
Average depth in centimeters
100
90
80
70
60
50
40
30
20
Avg. dia. (cm)
3
2
1
Number of burrows per M^2 x 100
70
60
50
40
30
20
10
5/7
6/18
7/17
8/20
9/17
10/15
5/21
7/2
8/6
9/3
10/1
10/29

Figure 35

Figure 35 A average burrow depth; B average burrow diameter; C number of burrows per 100 square meters; for all three transects by date in 1982. All values are the averaged sum of the primary and secondary transects. Sampling period June 4-6 not included.

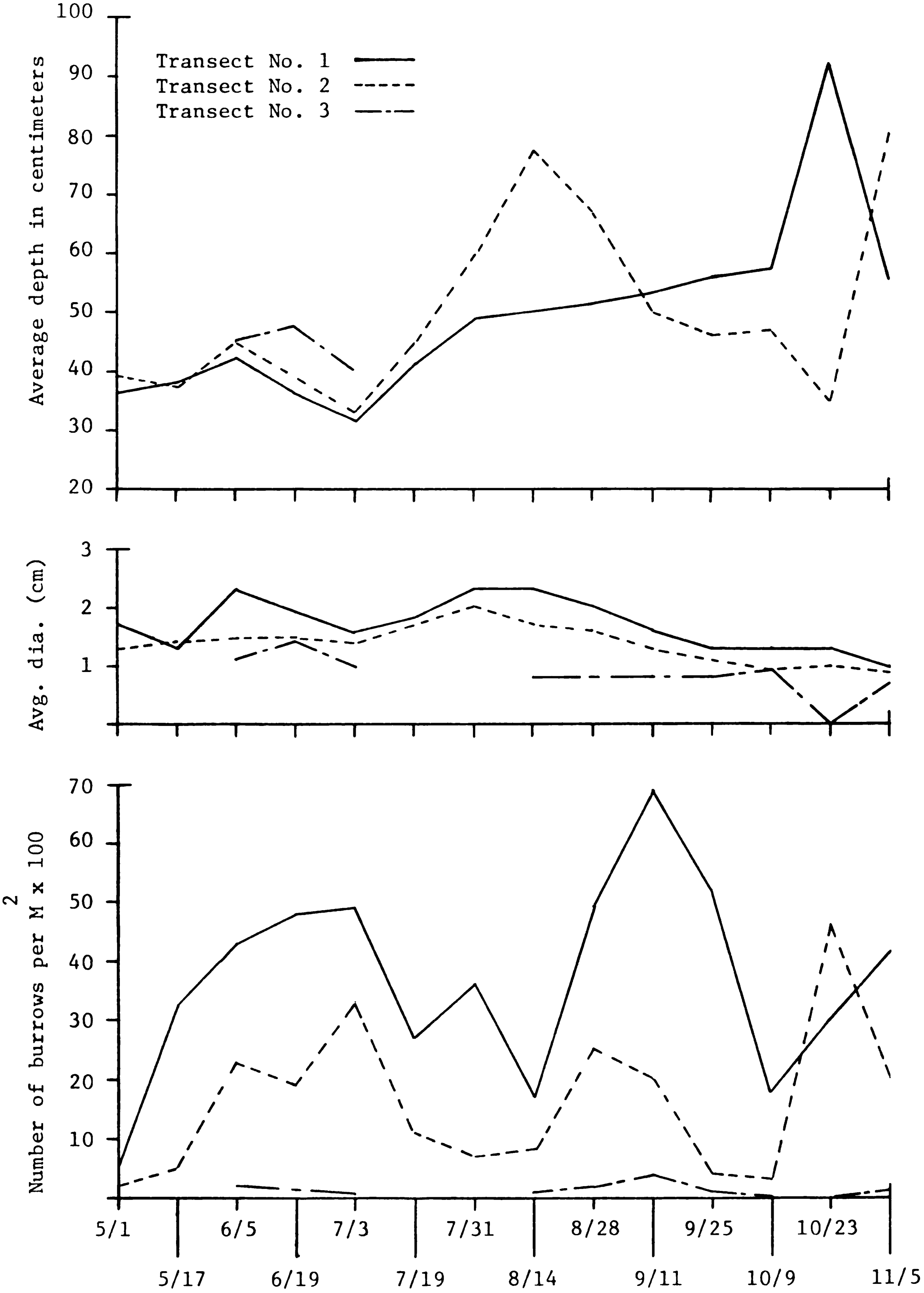

Transect No. 1
Transect No. 2
Transect No. 3
Average depth in centimeters
100
90
80
70
60
50
40
30
20
Avg. dia. (cm)
3
2
1
Number of burrows per M² x 100
70
60
50
40
30
20
10
5/1
6/5
7/3
7/31
8/28
9/25
10/23
5/17
6/19
7/19
8/14
9/11
10/9
11/5

Figure 34

Figure 34 A average burrow depth; B average burrow diameter; C number of burrows per 100 square meters; for all three transects by date of 1981. All values are the average sum of the primary and secondary transects.

A

B

Figure 36 Vegetation behind dunes; A transect 1; B transect 2; C transect 3.

C

Figure 36 (cont'd.)

The abundance of O. quadrata at transect 3 was so low that it could not be statistically compared to the control site. Crabs were recruited to this beach in both 1981 and 1982. However, they were usually found only in the section of the beach overwashed by the last high tide. As stated previously, the primary difference between this location and transect 2 was the level of ORV use.

In addition to the data gathered at transect 3, visual assessments of ghost crab activity along the section of the beach open to ORV's were made during each bi-weekly ORV use survey. These assessments showed an increase in crab activity from dune crossing No. 1 south to the Maryland/Virginia state line. This result correlates well with the vehicle use figures in Tables 11 and 12 and Figure 16. There was also a good correlation with the data reported by Steiner and Leatherman (1981) for their three surveys of this same section of beach (June 28, July 11 and August 8, 1978). They reported values of zero crabs per 0.1 hectare at the northern end (Dune Crossing No. 1) to 25 crabs at the southern end. Thus, on this section of the beach as vehicle use decreased, burrow densities increased.

Steiner and Leatherman (1981) reported three possible mechanisms by which ORV's could interfere with O. quadrata. The first was by crushing or burying them inside their burrows as vehicles passed overhead. It is unlikely that this is the causative factor since: 1) ghost crabs burrow below the 25 cm depth to which ORV passage can induce shear forces in the sand (Broadhead and Godfrey (1979); 2) ghost crabs regularly dig out of burrows filled by storms and, therefore, burying by vehicle passage should not present a problem; and 3) ghost crabs are quite resistant to crushing when run over by vehicles utilizing the backshore. However, if they were run over on the hard packed sand of the foreshore they were usually crushed (personal observation). Since most crab activity occurred on the backshore, the possibility of crushing by vehicles should not be a problem. The second mechanism proposed by Steiner and Leatherman (1981), was interruption of the crab's reproductive cycle. Although ORV use would undoubtedly impact reproductive activities, it is unlikely that this is the causative factor since: 1) on Assateague Island, and possibly other locations, recruitment of megalopae and first crab stages results from reproduction that occurred outside the experimental site; and 2) recruitment to the ORV zone (Figures 20&21, pages 74&78) occurred simultaneously with recruitment at the other two sample sites (transect 1 & 2). The final mechanism proposed was the modification of beach habitat by ORV's so that it was unable to support a ghost crab population. ORV traffic on the beach resulted in the compaction of sand at depth with an associated reduction in compaction in the immediate surface layer (Anders and Leatherman, 1981). These loosened surface sediments were more susceptible to aeolian activity (Zaremba, Godfrey and Leatherman, 1979). Broadhead and Godfrey (1979) stated that an important physical characteristic of beach sand was its ability to hold moisture beneath the surface. They reported that the sand remained moist because an evaporation barrier developed in the upper sand surface which prevented further loss of water once the upper layers dried out. ORV traffic destroyed this barrier, resulted in a more homogenous sand moisture profile and lead to an increased loss of moisture from the sand (Broadhead and Godfrey, 1979). Sand brought to the surface by ORV's dried out rapidly, and more ORV traffic resulted in even more dry sand being mixed with the moist sand below. Visual observations during this study at transects 1 and 2 revealed a "crust like" barrier layer which was rarely observed at transect 3. Thus, ORV induced impacts were the most likely explanation for reduced ghost crab populations in ORV zones on Assateague Island, Maryland, since: 1) recruits still arrived on the beach, but few adults were found; 2) ghost crabs can detect sand moisture and their burrows were concentrated within a preferred zone (Warburg & Shuchman, 1979); 3) ORV's travelling over the beach surface changed the moisture content of the sand creating a dry upper layer (Broadhead and Godfrey, 1979); and 4) O. quadrata cannot construct a burrow in dry sand (Letterman, 1973).

A gradient existed in numbers of burrows per square meter from the control at transect 1 through the heavily utilized ORV zone at transect 3, with numbers of burrows declining as human and vehicle use increased. Similar results regarding vehicle impacts on O. quadrata have been reported by Teerling (1970), Leggett & Butler (1975), Leggett (1975), Florschuts & Williams (1978), Britton (1979), Fisher and Tevesz (1979) and Steiner and Leatherman (1981). Since the availability of prey and physical factors which might influence O. quadrata selection of a location were similar at all three sites, human use impacts appeared to be responsible for the observed differences in abundance.

O. quadrata abundance was adversely impacted by ORV/human use along their entire range within the United States. In this study and in each of the studies reported in the literature, ghost crab abundance declined as human and/or ORV use increased, except for two studies conducted on the southern end of Assateague Island in Virginia. In these studies ghost crab abundance appeared to increase in conjunction with human use at a bathing beach. In addition, southern studies (Texas and Florida) indicated that _O. quadrata_ tended to aggregate near sources of human food (kitchens, trash containers, etc.) but this behavior was not observed on Assateague Island, Maryland. In general, however, _O. quadrata_ populations in both northern and southern locations were adversely impacted by human and ORV use of the beach.

SUMMARY

The present study was the first in-depth investigation of the ecology of _O. quadrata_ on Assateague Island, Maryland which relates the impacts of various types of human uses to changes in life history and reductions in abundance. Three experimental locations were selected which represented different levels of human use: Heavy - ORV traffic and all other associated human uses; Moderate - official vehicle traffic and day-use from the adjoining campground; and Light - almost no vehicle traffic and only hiking use by park visitors. Sand grain size, beach profiles, temperature, wind direction/velocity, precipitation and prey availability were evaluated to determine any differences in the study sites and to ensure that some factor or factors other than human use was not responsible for any observed life history changes or reductions in abundance.

1. Physical

Sand grain size, beach profiles, temperature, wind direction and velocity and precipitation were similar at all three experimental sites. Ghost crabs did not select one location over another as a result of differences in these physical characteristics. Human use impacts at these locations, however, did alter the habitat.

2. Biological

A. Mole Crab:

There was no difference in _E. talpoida_ abundance or population structure at the three experimental sites. Mole crabs were abundant during the entire period of _O. quadrata_ forebeach activity (May-November) 1981 and (May-October) 1982 and were the primary species preyed upon by _O. quadrata_. Few _Donax_ sp. were found during these surveys although they were a more important and abundant prey species in North Carolina (Wolcott, 1978).

B. Ghost Crab:

1. _Reproduction_

O. quadrata was reproductively active on Assateague Island, Maryland, from June through September. Copulation was observed only outside the burrow near the water's edge at night and appeared to be correlated with the time of the new moon. Mound construction associated with larger burrows was observed in both 1981 and 1982, although it was not conclusively related to reproductive activity. Although specialized burrows have been linked to reproductive activity in other _Ocypode_ species, no such relationship was observed on Assateague Island. Stridulation and/or visual displays were never noted during the study, although agonistic displays were common. Air-borne chemical cues could be involved in male/female detection during reproductive periods.

2. _Recruitment_

Meglopae and first crabs were recruited to the study sites almost continuously, beginning in May, with the major recruitment occurring from mid-August to the end of October. The exact mechanism by which _O. quadrata_ is recruited to Assateague Island is not well understood. Data collected strongly indicate there was a major reproductive source outside the Assateague area. The counter-current hypothesis proposed by Efford (1970) for recruitment of _E. analoga_ appeared to provide a logical explanation for recruitment of larval _O. quadrata_ which may be caught in and carried north by the Gulf Stream. Spin-off eddies (warm core rings) and atmospheric forcing move the larval forms into the south-flowing Virginia Current from which they could then be moved shoreward by onshore drift along the seafloor.

3. Growth

Growth was not measured directly, but was estimated from shifts between size classes as the year progressed. There was clearly an increase in the numbers of crabs in the four larger size classes. A 12% increase in size between moults was calculated, using measurements from crabs captured in July and August 1982. This increase in size was lower than the rates reported for other species of _Ocypode_. Ambient temperatures may be the critical factor in the growth of _O. quadrata_ on Assateague island. It can prolong the period of proecdysis and shorten the yearly activity period.

4. Burrow Construction

Burrows constructed by _O. quadrata_ on Assateague Island were of three general types; "Y"-shaped, unbranched tunnel (straight, slightly-arched or "J"-shaped) and "U"-shaped. They served as protection from desiccation, predators and conspecifics. Burrow construction was performed similar to that reported in the literature, with crabs testing a number of locations prior to commencing construction. Sand removed during construction was scattered in a fan-like pattern, left in small pellets or piled in a mound. Mounds were almost always associated with larger burrows. Crabs frequently constructed plugs in burrow entrances during mid-day in warmer months.

5. Distribution on the Beach

Crabs initially became active behind the dunes and on the upper section of the backshore. As summer progressed, crabs migrated toward the foreshore and became concentrated near the crest of the berm. The process was reversed in the fall. This pattern was most evident in the larger crabs.

6. Activity Period

Crabs were active on Assateague Island from mid-April through November, 1981 and from mid-April through October, 1982. Activity on the forebeach (backshore and foreshore) occurred from May through November, 1981 and from May through October, 1982. Crabs at transect 1 were diurnally and nocturnally active with their major activity period occurring from about dusk to 0800 hours the following morning. Minor activity periods occurred from 0800 to 1200 hours and from 1600 hours to dusk. Feeding was the primary activity engaged in during the major period. Burrow maintenance and wandering occurred during both minor periods. Juveniles tended to be more active toward the beginning and end of the major activity period. Activity patterns were disrupted by weather events and human intrusion.

7. Food/Feeding

O. quadrata on Assateague Island was primarily a predator, feeding principally on the mole crab E. talpoida. O. quadrata was not observed feeding on Donax sp. which was a common component of the beach fauna to the south of Assateague Island. They were preyed upon by ghost crabs in North Carolina (Wolcott, 1978) and Inhaca Island, Mocambique (Hughes, 1966). Ghost crabs were, however, omnivorous faculative scavengers, feeding on virtually any food source available. Mole crabs were captured in the overwash zone and consumed on the crest of the berm or near the burrow entrance. Mole crabs were apparently located with the aid of tactile hairs on O. quadrata's walking legs or possibly through chemical stimulation of the chela. No observations of deposit-feeding and resultant formation of pseudofecal pellets were noted. O. quadrata was observed dragging food items into its burrow. Cannibalism was observed but not prevalent.

8. Predators

O. quadrata, on Assateague Island, was preyed upon by the red fox, V. fulva. The red fox was a regular predator on O. quadrata based on the number of digs, and the presence of ghost crab remains in fox scat. Ghost crabs avoided predation by seeking refuge in burrows, entering the ocean or burying under the surface of the sand.

9. Human Use Impacts

The abundance and activity period of O. quadrata on Assateague Island were adversely impacted by various human uses occurring within the National Park. The most detrimental activity was the use of the beach by ORV's. ORV use of the beach alters the sand moisture content, results in drying of the surface sand layer and destruction of the moisture barrier. The dry surface layer was more susceptible to aeolian transport. Consequently, ghost crab abundance was reduced to zero in the northern most section of the beach open to this activity. ORV impacts decreased southward to the Maryland/Virginia state line, although the abundance of ghost crabs did not appear to approach the level noted for the control site (transect 1). Ghost crab abundance was also lower at the moderately impacted beach (transect 2), although this location had a size class distribution similar to the control site.

CONCLUSIONS

This study found that _O. quadrata_ ecology on Assateague Island was similar to that reported in the literature for more southern populations (North Carolina and Texas). Thus, the first part of the hypothesis was accepted. In addition, since _O. quadrata_ was adversely impacted by human use, the second part of the hypothesis was also accepted.

The major conclusions of this study are:

1. _O. quadrata_ copulates outside the burrow near the water's edge at night.
2. First crabs recruited to Assateague Island most likely came from a source other than the resident adults.
3. Growth on Assateague appeared to be slower than that reported in the literature for other members of the family (12% vs 16-20%).
4. Crabs at transect 1 (control) were diurnally and nocturnally active while those at transect 2 were primarily nocturnally active.
5. _O. quadrata_ on Assateague Island was primarily a predator, feeding principally on _E. talpoida_.
6. Red fox, _V. fulva_, was a regular predator on _O. quadrata_.
7. The activity period and abundance of _O. quadrata_ were adversely impacted by human use of the beach.

8. ORV impacts were most severe completely eliminating *O. quadrata* from transect 3.

APPENDIX

Table 1

Average air temperatures (in degrees Centigrade) and total precipitation (in centimeters) recorded at Salisbury and Snow Hill, Maryland, and Rehoboth Beach, Delaware*

Air Temperatures

Month	Salisbury	Snow Hill	Rehoboth Beach	Average
January	3.7	3.4	2.3	3.1
February	4.1	3.7	2.7	3.5
March	7.6	7.1	6.5	7.1
April	13.1	12.6	11.7	12.4
May	18.4	17.8	16.6	17.6
June	23.0	22.6	21.5	22.3
July	25.2	24.8	24.1	24.7
August	24.5	24.0	23.2	23.9
September	21.0	20.7	19.9	20.6
October	15.2	14.9	14.6	14.9
November	9.6	9.1	8.9	9.2
December	4.2	4.1	3.2	3.8
Annual	14.2	13.7	13.0	13.6

Precipitation

Month	Salisbury	Snow Hill	Rehoboth Beach	Average
January	9.30	10.01	9.17	9.50
February	8.15	8.71	8.26	8.38
March	10.95	11.73	10.26	10.97
April	8.48	9.17	10.95	8.69
May	9.19	9.17	10.13	9.50
June	8.86	9.65	9.78	9.47
July	11.15	13.00	11.61	11.91
August	15.27	14.40	12.57	14.07
September	11.28	11.43	9.09	10.59
October	8.89	9.93	8.00	8.94
November	8.15	9.02	9.80	8.99
December	7.95	8.66	9.22	8.61
Annual	117.17	128.89	115.49	119.18

---

*From E.P.A. (1977)

Table 3

Mole Crab Size Class Data (6/27/86)

Size	Length (mm)			Width (mm)			% Gravid	Number
	Mean	SD	SE	Mean	SD	SE		
Large	29.2	2.2	0.2	16.3	1.4	0.1	82	100
Medimum	18.9	1.6	0.2	10.3	0.9	0.1	53	100
Small	14.6	0.9	0.1	7.4	0.5	0.1	0	100

Table 4

Phi class data and associated standard deviations
for each transect and sample location by date

Sample location on beach

		1		2		3		4		5		6	
		Phi	SD	Phi	SD	Phi	SD	Phi	SD	Phi	SD	Phi	SD
Date	1	1.87	0.36	1.74	0.34	1.71	0.41	1.70	0.47	- M* -		-	-
7/19/79	2	1.65	0.41	1.38	0.48	1.37	0.49	1.66	0.46	1.34	0.62	-	-
	3	1.95	0.36	1.62	0.43	1.46	0.56	1.48	0.50	1.52	0.53	-	-
8/14/81	1	- M -		1.72	0.37	1.66	0.39	- M -		1.87	0.51	-	-
	2	1.70	0.40	- M -		1.07	0.65	1.36	0.51	- M -			
	3	1.65	0.50	1.49	0.66	1.52	0.66	1.56	0.47	- M -			
12/08/81	1	1.85	0.37	1.66	0.39	- M -		- M -		1.75	0.51	-	-
	2	- M -		1.68	0.38	1.64	0.32	1.46	0.41	1.74	0.40	-	-
	3	1.80	0.39	1.79	0.27	1.81	0.39	1.46	0.49	1.80	0.47	-	-
5/11/82	1	1.93	0.32	1.72	0.38	1.68	0.43	1.68	0.40	1.42	0.48	-	-
	2	1.91	0.33	1.34	0.51	1.48	0.46	1.54	0.39	1.04	0.57	-	-
	3	1.80	0.52	1.81	0.36	1.47	0.69	1.62	0.41	1.53	0.38	1.59	0.45
10/1/82	1	1.67	0.34	1.07	0.53	1.57	0.41	- M -		- M -			
	2	1.65	0.43	1.38	0.48	1.01	0.62	1.29	0.50	- M -			
	3	1.61	0.42	1.46	0.48	1.42	0.59	1.39	0.48	1.49	0.40		

* M - Sample Label Destroyed

Table 5

Phi class and corresponding grain size in milimeters (mm)

Phi Class	Grain Size MM	Sediment Type
-1.0	2.00	
-0.75	1.68	Very coarse
-0.5	1.41	sand
-0.25	1.19	
0.0	1.00	
0.25	0.84	
0.5	0.71	Coarse
0.75	0.59	sand
1.0	0.50	
1.25	0.42	
1.5	0.35	Medium
1.75	0.30	Sand
2.0	0.25	
2.25	0.210	
2.5	0.177	Fine
2.75	0.149	Sand
3.0	0.125	
3.25	0.105	
3.5	0.088	Very Fine
3.75	0.074	Sand
4.0	0.0625	

Table 6

Temperature (Centigrade)
and
wind data (Knots)

1981

Date	Temperature		Wind	
	Air	Water	Direction	Velocity
1/1	-1.1	2.8	NE	10
1/15	0.6	-1.1	NE	8
2/1	-5.0	3.3	SSW	4
2/15	-5.0	3.3	SSW	4
3/1	8.9	2.2	N	10
3/15	0.0	3.3	WWSW	10
4/1	8.9	6.7	SSE	6
4/17	17.2	10.0	WSW	17
5/3	15.0	12.2	N	8
5/16	16.1	13.9	NW	13
6/6	20.6	16.7	SW	9
6/19	21.1	20.0	ESE	10
7/3	21.1	20.0	ENE	8
7/18	25.6	21.7	NE	7
8/1	26.1	21.7	NE	9
8/14	22.2	21.7	W	8
8/29	21.7	21.1	ENE	7
9/11	17.2	21.1	SW	10
9/25	10.0	21.1	NW	9
10/9	8.9	17.8	NW	10
10/23	15.6	17.8	S	11
11/5	15.6	14.4	NW	12
11/15	8.3	14.4	NW	18
12/1	0.0	8.9	NW	10
12/15	2.8	6.7	NW	8

Table 7

Temperature (Centigrade)
and
wind data (Knots)

1982

Date	Temperature		Wind	
	Air	Water	Direction	Velocity
1/3	2.8	2.8	SSE	6
1/15	-6.7	0.0	SE	11
2/3	5.0	3.9	SE	8
2/15	5.0	3.3	S	8
3/3	3.3	2.2	NNE	12
3/15	7.7	3.3	N	8
4/3	7.8	7.8	SSE	11
4/13	9.4	6.7	SSW	11
4/23	3.9	10.0	NW	14
5/7	15.0	13.9	S	3
5/21	16.7	18.3	WSW	6
6/2 *	19.4	17.2	W	10
6/18	21.1	22.8	W	7
7/3	20.6	22.8	ENE	5
7/17	24.4	21.1	SW	4
8/7	22.8	21.7	ENE	5
8/20	22.8	21.1	SW	10
9/3	22.2	21.1	SSW	15
9/17	17.8	18.3	NNE	15
10/2	15.0	18.9	NNE	12
10/15	16.7	16.7	W	10
10/29	10.0	12.8	W	5
11/12	13.9	12.8	SSW	12

* Sample Period 6/1-6/82 lost to poor weather

Table 8

Air surface* & undersand temperatures
(Centigrade) measured at
Transect No. 1 in 1982/83

Date	Pipe		Buried	
	Surface	Under	Surface	Under
		1982		
4/13	17.2	8.9	17.8	8.9
4/18**	26.1	11.1	28.9	11.1
4/23	12.2	11.1	12.2	10.0
5/7	15.6	13.3	15.0	12.2
5/11	17.2	13.9	18.3	13.3
6/11	23.3	16.7	22.8	16.7
6/18	24.4	17.8	25.0	17.8
7/2	26.1	20.0	27.2	19.4
7/17	31.7	21.7	31.7	20.6
8/6	23.9	21.7	24.4	20.6
8/20	23.9	21.1	24.4	20.6
9/4	17.8	20.6	18.9	20.0
9/17	17.8	20.0	18.3	19.4
10/2	17.2	18.9	17.2	19.4
10/16	11.1	18.3	12.2	18.3
10/29	13.9	15.0	14.4	15.6
11/2	21.1	16.1	16.7	17.2
11/12	15.0	14.4	15.0	16.1
11/30	15.0	12.2	15.0	15.0
		1983		
1/5	7.8	7.7	7.8	11.7
3/19	16.1	8.9	Lost	
4/16	7.8	10.0	8.3	10.0
5/1	18.3	12.2	20.6	12.2

* Approximately 12 inches above surface of sand

** Taken at 2:15 pm with no protective box on unit

Table 9

Visitor use in 1981 from Park Service records

Month 1981	Entrance Traffic Count	ORV Traffic Count	No. Campsites Occupied	No. of Camp Site Days Available	No. of Campers
January	3,016	100*	-	-	-
February	2,864	96	-	-	-
March	4,934	286	-	-	-
April**	9,616	612	354	560	1,064
May**	22,049	983	1,526	3,734	4,052
June	30,099	1,342	2,989	3,780	7,548
July	33,730	1,463	4,213	3,906	12,465
August	33,312	1,497	4,428	3,906	14,191
September	15,846	690	2,287	3,780	6,040
October***	12,857	813	398	1,240	-
November	8,940	570	162	1,200	-
December	2,439	421	38	1,240	-

* Incomplete

** Bayside opened April 17; north beach opened May 3, 1981

*** Only bayside remained open after September 30

Table 10
Visitor use in 1982 from Park Service records

Month 1982	Entrance Traffic Count	ORV Traffic Count	No. Campsites Occupied	No. of Camp Site Days Available	No. of Campers
January	2,553	248	26	1,240	-
February	2,687	120	30	1,120	-
March	4,512	233	94	1,240	-
April	9,405	485	429	1,200	546
May*	12,974	962	1,169	1,710	2,287
June	27,230	1,601	2,006	3,780	5,584
July	56,763	1,893	3,723	3,906	11,512
August	45,828	2,148	3,829	3,906	12,220
September**	27,780	1,300	2,292	3,780	5,736
October	11,793	747	840	1,240	-
November	5,132	374	192	1,200	-
December	2,013	433	56	1,240	-

* North Beach opened May 27, 1982

** North Beach closed September 30, 1982

Table 11

Human use in ORV zone 1981

	Section 1					Section 2				
	*Vh	Fi	Sw	Wa	O	Vh	Fi	Sw	Wa	O
7/4/81	10	4	0	0	3	3	5	0	2	0
7/18/81	76	57	34	5	125	28	11	7	6	38
7/31/81	20	10	17	10	25	4	0	2	0	0
8/15/81	21	15	17	11	29	8	8	2	7	4
8/29/81	28	30	3	19	39	12	10	0	0	20
9/12/81	23	20	2	16	21	10	8	1	1	12
9/26/81	25	35	4	9	23	7	4	4	2	5
10/10/81	10	20	0	2	0	4	8	0	2	0
10/24/81	4	11	0	10	0	3	4	0	0	0
11/6/81	1	2	0	0	0	0	0	0	0	0
TOTAL	-	204	104	82	265	-	58	16	20	79
%	-	31	16	13	40	-	34	9	12	45

* Vh, vehicles; Fi, fishing; Sw, swimming; Wa, walking; O, other.

Table 12
Human use in ORV zone 1982

	Section 1					Section 2				
	*Vh	Fi	Sw	Wa	O	Vh	Fi	Sw	Wa	O
4/24/82	11	5	0	13	10	8	4	0	0	4
5/8/82	17	13	0	10	0	4	5	0	0	0
5/22/82	Not Taken Rain									
6/4/82	"	"	"	Entire Sampling Period Lost						
6/19/82	35	33	11	5	62	14	8	0	1	8
7/3/82	48	41	14	8	67	15	10	3	5	23
7/17/82	59	31	25	2	83	22	15	9	0	23
8/6/82	Lost truck failure									
8/21/82	56	57	12	21	94	17	11	11	0	13
9/4/82	61	85	8	10	87	8	10	0	3	8
9/18/82	27	43	0	8	18	8	7	0	2	7
10/2/82	19	28	10	21	15	24	6	0	0	38

Table 12 (cont'd.)

10/16/82	18	27	0	2	10	3	0	0	0	2
10/29/82	7	7	0	4	3	6	4	0	0	1
11/12/82	1	1	0	0	0	0	0	0	0	0
TOTAL	-	371	80	104	449	-	80	23	11	127
%	-	37	8	10	45	-	33	10	5	52

*Vh, vehicles; Fi, fishing; Sw, swimming; Wa, walking; O, other

Table 13

Mole Crab Census 1981

Transect 1

Sample Date	Number Small	Number Medium	Number Large	Total	Mean	Moon Phase
5/17*	65	-	216	281	94	F
6/5	21	7	11	39	13	N
6/19	20	6	1	27	9	F
7/3	1	2	1	4	1	N
7/18	95	85	6	186	62	F
7/31	19	45	112	176	59	N
8/15	38	52	32	122	41	F
8/28	54	211	129	394	131	N
9/12	12	54	96	162	54	F
9/25	14	82	59	155	52	N
10/9	11	35	35	81	27	F
10/24	4	17	16	37	12	N
11/5	3	8	39	50	17	F

*Medium + Large Listed Together

Table 13 (cont'd.)

Transect 2

Sample Date	Number Small	Number Medium	Number Large	Total	Mean	Moon Phase
5/17*	74	-	167	241	80	F
6/5	17	21	49	87	29	N
6/19	19	7	6	32	11	F
7/3	41	57	36	136	45	N
7/18	39	45	17	101	34	F
7/31	75	121	77	273	91	N
8/15	61	204	126	391	130	F
8/28	31	112	94	237	79	N
9/12	6	32	15	53	18	F
9/25	10	81	53	144	48	N
10/9	29	31	22	82	27	F
10/24	3	6	32	41	14	N
11/5	2	11	45	58	19	F

Table 13 (cont'd.)

Transect 3

Sample Date	Number Small	Number Medium	Number Large	Total	Mean	Moon Phase
5/17*	58	-	79	137	46	F
6/5	67	53	28	148	49	N
6/19	11	8	3	22	7	F
7/3	101	90	20	211	70	N
7/18	25	21	13	59	20	F
7/31	68	148	36	252	84	N
8/15	39	168	78	285	95	F
8/28	13	120	104	237	79	N
9/12	10	36	85	131	44	F
9/25	7	33	101	141	47	N
10/9	32	45	42	119	40	F
10/24	3	7	21	31	10	N
11/5	3	2	13	18	6	F

Table 14

Mole Crab Census 1982

Transect 1

Sample Date	Number Small	Number Medium	Number Large	Total	Mean	Phase Moon
4/23	0	1	0	1	0	N
5/7	18	27	43	88	29	F
5/21	10	16	15	41	14	N
6/19	3	13	31	47	16	N
7/2	18	20	11	49	16	F
7/17	58	60	42	160	53	N
8/7	11	8	6	25	8	F
8/21	81	266	190	537	179	N
9/3	0	22	132	154	51	F
9/17	1	2	18	21	7	N
10/1	22	23	25	70	23	F
10/15	27	28	13	68	23	N
10/29	72	66	35	173	58	F

Table 14 (cont'd.)

Transect 2

1982 Sample Date	Number Small	Number Medium	Number Large	Total	Mean	Moon Phase
4/23	0	2	6	8	3	N
5/7	21	36	39	96	32	F
5/21	12	8	9	29	10	N
6/19	21	42	41	104	35	N
7/2	53	62	24	139	46	F
7/17	41	54	88	183	61	N
8/7	13	28	29	70	23	F
8/21	10	59	105	174	58	N
9/3	8	45	98	151	50	F
9/17	4	4	15	23	8	N
10/1	9	11	19	39	13	F
10/15	64	53	17	134	45	N
10/29	54	27	36	117	39	F

Table 14 (cont'd.)

Transect 3

1982 Sample Date	Number Small	Number Medium	Number Large	Total	Mean	Moon Phase
4/23	9	10	12	31	10	N
5/7	24	27	27	78	26	F
5/21	22	36	18	76	25	N
6/19	5	20	24	49	16	N
7/2	17	19	12	48	16	F
7/17	25	33	16	74	25	N
8/7	20	62	15	97	32	F
8/21	1	34	190	225	75	N
9/3	4	60	110	174	58	F
9/17	2	9	2	13	4	N
10/1	28	17	31	76	25	F
10/15	45	59	75	179	60	N
10/29	49	41	59	149	50	F

Table 16

Ghost Crab Census

Transect 1 1981

PRIMARY

Date	B	MS	SD	SE	MD	N*	SD	SE	SM	MF
4/17	0	0	0	0	0	0	0	0	0	F
5/1	7	1.9	1.15	0.44	33.5	6	10.82	4.42	0.09	N
5/17	24	1.1	0.28	0.06	33.2	23	11.99	2.50	0.38	F
6/5	29	2.2	1.32	0.25	38.1	24	16.43	3.35	0.40	N
6/19	43	1.9	1.10	0.17	35.7	31	15.58	2.80	0.48	F
7/3	48	1.5	0.72	0.10	32.3	37	18.34	3.01	0.59	N
7/19	18	1.8	1.02	0.24	50.3	12	26.68	7.70	0.22	F
7/31	16	2.5	0.89	0.22	50.3	16	28.27	7.07	0.20	N
8/14	10	2.4	1.01	0.32	39.0	8	17.12	6.05	0.11	F
8/28	37	1.8	0.95	0.16	51.7	21	26.06	5.69	0.46	N
9/11	46	1.5	1.20	0.18	52.3	12	21.49	6.21	0.85	F
9/25	35	1.2	0.85	0.14	60.0	6	32.17	13.13	0.56	N
10/9	15	1.2	0.60	0.16	50.4	7	10.34	3.91	0.17	F
10/23	41	1.1	0.90	0.14	64.4	5	36.39	16.27	0.51	N
11/5	23	0.9	0.15	0.03	52.0	1	0	0	0.51	F
11/17	0	0	0	0	0	0	0	0	0	N

B, Number of Burrows; MS, Mean Size (Dia.); MD, Mean Depth;
SM, Number per square meter; MF, Moon Phase
* Number used to calculate Mean Depth
\- No depth values taken burrows under 1.0 cm in diameter

Table 16 (cont'd.)

SECONDARY

Date	B	MS	SD	SE	MD	N*	SD	SE	SM	MF
4/17	0	0	0	0	0	0	0	0	0	F
5/1	2	1.3	0.35	0.25	42.5	2	3.54	2.50	0.02	N
5/17	17	1.6	0.78	0.19	42.1	15	15.52	4.00	0.27	F
6/5	29	2.5	1.33	0.25	48.2	17	17.19	4.17	0.46	N
6/19							MISSING			
7/3	31	1.6	0.81	0.14	30.0	31	15.31	2.75	0.38	N
7/19	25	1.8	0.66	0.13	37.1	25	16.61	3.32	0.31	F
7/31	42	2.2	0.95	0.15	47.9	28	18.29	3.46	0.52	N
8/14	20	2.2	1.24	0.28	55.0	16	32.00	8.00	0.22	F
8/28	33	2.2	1.07	0.19	51.2	25	21.45	4.29	0.52	N
9/11	28	1.9	1.17	0.22	54.5	17	27.58	6.69	0.52	F
9/25	30	1.5	0.97	0.18	53.5	10	13.46	4.26	0.48	N
10/9	15	1.3	0.53	0.14	66.8	5	17.63	7.88	0.19	F
10/23	5	2.5	1.87	0.84	137.3	3	5.77	3.33	0.07	N
11/5	14	1.2	0.93	0.25	57.0	2	14.14	10.00	0.31	F
11/17	0	0	0	0	0	0	0	0	0	N

Table 16 (cont'd.)

COMBINED

Date	B	MS	SD	SE	MD	N*	SD	SE	SM	MF
4/17	0	0	0	0	0	0	0	0	0	F
5/1	9	1.7	1.04	0.35	35.8	8	10.14	3.58	0.06	N
5/17	41	1.3	0.51	0.09	36.7	38	14.00	2.27	0.33	F
6/5	58	2.3	1.33	0.17	42.3	41	17.29	2.70	0.43	N
6/19	43	1.9	1.10	0.17	35.7	31	15.58	2.80	0.48	F
7/3	79	1.6	0.75	0.08	31.3	68	16.94	2.05	0.49	N
7/19	43	1.8	0.82	0.13	41.4	37	21.00	3.45	0.27	F
7/31	58	2.3	0.94	0.12	48.8	44	22.14	3.34	0.36	N
8/14	30	2.3	1.15	0.21	49.7	24	28.58	5.83	0.17	F
8/28	70	2.0	1.02	0.12	51.4	46	23.39	3.45	0.49	N
9/11	74	1.6	1.20	0.14	53.6	29	24.85	4.61	0.69	F
9/25	65	1.3	0.91	0.11	55.9	16	21.55	5.39	0.52	N
10/9	30	1.3	0.56	0.10	57.4	12	15.51	4.48	0.18	F
10/23	46	1.3	1.11	0.16	91.8	8	46.81	16.55	0.30	N
11/5	37	1.0	0.58	0.10	55.3	3	10.41	6.01	0.41	F
11/17	0	0	0	0	0	0	0	0	0	N

Table 17

Ghost Crab Census

Transect 2 1981

					PRIMARY					
Date	B	MS	SD	SE	MD	N*	SD	SE	SM	MF
4/17	0	0	0	0	0	0	0	0	0	F
5/1	8	1.4	0.35	0.12	39.0	8	13.19	4.66	0.05	N
5/17	7	1.4	0.18	0.06	35.9	7	10.02	3.79	0.06	F
6/5	46	1.5	0.66	0.09	46.6	44	22.98	3.46	0.28	N
6/19	36	1.4	0.21	0.03	35.6	36	11.92	1.99	0.22	F
7/3	56	1.4	0.44	0.06	30.6	48	17.62	2.54	0.39	N
7/19	14	1.7	0.40	0.11	51.2	13	31.87	8.84	0.08	F
7/31	15	2.0	0.71	0.18	58.0	14	33.06	8.84	0.09	N
8/14	10	1.5	0.99	0.31	82.4	5	63.30	28.30	0.06	F
8/28	33	1.6	0.85	0.15	64.9	17	32.28	7.83	0.26	N
9/11	29	1.2	0.57	0.11	36.7	10	18.48	5.84	0.18	F
9/25	1	0.8	0.0	0.0	-	-	-	-	0.01	N
10/9	4	0.8	0.05	0.02	-	-	-	-	0.02	F
10/23	69	1.0	0.25	0.03	35.1	12	11.08	3.20	0.48	N
11/5	32	1.0	0.31	0.06	95.0	4	32.77	26.39	0.25	F
11/17	0	0	0	0	0	0	0	0	0	N

B, Number of Burrows; MS, Mean Size (Dia.); MD, Mean Depth;
SM, Number Per Square Meter; MF, Moon Phase
* Number used to calculate Mean Depth
\- No depth values taken burrows under 1.0 cm in diameter

Table 17 (cont'd.)

SECONDARY

Date	B	MS	SD	SE	MD	N*	SD	SE	SM	MF
4/17	0	0	0	0	0	0	0	0	0	F
5/1	5	1.3	0.11	0.05	38.8	5	6.91	3.09	0.03	N
5/17	5	1.4	0.16	0.07	38.8	4	5.56	2.78	0.04	F
6/5	30	1.5	0.42	0.08	42.3	29	22.69	4.21	0.19	N
6/19	27	1.6	0.83	0.16	41.7	27	27.78	4.19	0.17	F
7/3	38	1.4	0.34	0.05	37.1	33	22.39	3.90	0.26	N
7/19	22	1.7	0.59	0.13	41.0	21	17.40	3.80	0.13	F
7/31	8	2.1	0.43	0.15	61.3	8	18.72	6.62	0.05	N
8/14	15	1.8	1.18	0.31	73.3	6	40.66	16.60	0.09	F
8/28	30	1.6	0.83	0.15	68.7	14	39.29	10.50	0.24	N
9/11	32	1.3	0.80	0.14	59.6	14	30.23	8.08	0.22	F
9/25	10	1.1	0.51	0.16	46.2	5	41.79	18.69	0.07	N
10/9	5	1.0	0.23	0.10	47.0	1	0	0	0.03	F
10/23	64	1.0	0.56	0.07	34.5	6	16.18	6.61	0.44	N
11/5	19	0.9	0.13	0.03	22.0	1	0	0	0.15	F
11/17	0	0	0	0	0	0	0	0	0	N

Table 17 (cont'd.)

COMBINED

Date	B	MS	SD	SE	MD	N*	SD	SE	SM	MF
4/17	0	0	0	0	0	0	0	0	0	F
5/1	13	1.3	0.28	0.08	38.9	13	10.84	3.01	0.04	N
5/17	12	1.4	0.17	0.09	36.9	11	8.47	2.55	0.05	F
6/5	76	1.5	0.58	0.07	44.9	73	22.81	2.67	0.23	N
6/19	63	1.5	0.57	0.07	38.2	63	16.99	2.14	0.19	F
7/3	94	1.4	0.40	0.04	33.2	81	19.81	2.20	0.33	N
7/19	36	1.7	0.52	0.09	44.9	34	24.04	4.12	0.11	F
7/31	23	2.0	0.62	0.13	59.2	22	28.21	0.02	0.07	N
8/14	25	1.7	1.10	0.22	77.5	11	49.51	14.93	0.08	F
8/28	63	1.6	0.84	0.11	66.6	31	35.05	6.30	0.25	N
9/11	61	1.3	0.70	0.09	50.1	24	27.99	5.71	0.20	F
9/25	11	1.1	0.50	0.15	46.2	5	41.79	18.69	0.04	N
10/9	9	0.9	0.04	0.19	47.0	1	0	0	0.03	F
10/23	113	1.0	0.43	0.04	34.9	18	12.51	2.95	0.46	N
11/5	51	0.9	0.26	0.04	80.4	5	56.16	25.12	0.20	F
11/17	0	0	0	0	0	0	0	0	0	N

Table 18

Ghost Crab Census

Transect 3 1981

PRIMARY

Date	B	MS	SD	SE	MD	N*	SD	SE	SM	MF
4/17	0	0	0	0	0	0	0	0	0	F
5/1	0	0	0	0	0	0	0	0	0	N
5/17	0	0	0	0	0	0	0	0	0	F
6/5	3	1.2	0.29	0.17	35.7	3	27.93	16.13	0.02	N
6/19	2	1.4	0.07	0.05	47.5	2	4.95	3.50	0.01	F
7/3	0	0	0	0	0	0	0	0	0	N
7/19	0	0	0	0	0	0	0	0	0	F
7/31	0	0	0	0	0	0	0	0	0	N
8/14	2	0.8	0	0	-	-	-	-	0.01	F
8/28	3	0.8	0.06	0.03	-	-	-	-	0.02	N
9/11	8	0.8	0.13	0.05	-	-	-	-	0.05	F
9/25	2	0.8	0.07	0.05	-	-	-	-	0.01	N
10/9	0	0	0	0	0	0	0	0	0	F
10/23	0	0	0	0	0	0	0	0	0	N
11/5	2	0.8	0.21	0.15	-	-	-	-	0.01	F
11/17	0	0	0	0	0	0	0	0	0	N

B, Number of Burrows; MS, Mean Size (Dia.); MD, Mean Depth;
SM, Number Per Square Meter; MF, Moon Phase
* Number used to calculate Mean Depth
\- No depth values taken burrows under 1.0 cm in diameter

Table 18 (cont'd.)

SECONDARY

Date	B	MS	SD	SE	MD	N*	SD	SE	SM	MF
4/17	0	0	0	0	0	0	0	0	0	F
5/1	0	0	0	0	0	0	0	0	0	N
5/17	0	0	0	0	0	0	0	0	0	F
6/5	4	1.1	0.15	0.08	51.5	4	24.45	12.22	0.02	N
6/19	0	0	0	0	0	0	0	0	0	F
7/3	1	1.0	0	0	40.0	1	0	0	0.01	N
7/19	0	0	0	0	0	0	0	0	0	F
7/31	0	0	0	0	0	0	0	0	0	N
8/14	0	0	0	0	0	0	0	0	0	F
8/28	2	0.8	0.07	0.05	-	-	-	-	0.01	N
9/11	7	0.8	0.04	0.08	-	-	-	-	0.04	F
9/25	0	0	0	0	0	0	0	0	0	N
10/9	2	0.9	0.07	0.05	-	-	-	-	0.01	F
10/23	0	0	0	0	0	0	0	0	0	N
11/5	1	0.7	0	0	-	-	-	-	0.01	F
11/17	0	0	0	0	0	0	0	0	0	N

Table 18 (cont'd.)

COMBINED

Date	B	MS	SD	SE	MD	N*	SD	SE	SM	MF
4/17	0	0	0	0	0	0	0	0	0	F
5/1	0	0	0	0	0	0	0	0	0	N
5/17	0	0	0	0	0	0	0	0	0	F
6/5	7	1.1	0.20	0.07	44.7	7	25.11	9.49	0.02	N
6/19	2	1.4	0.07	0.05	47.5	2	4.95	3.50	0.01	F
7/3	1	1.0	0	0	40.0	1	0	0	0	N
7/19	0	0	0	0	0	0	0	0	0	F
7/31	0	0	0	0	0	0	0	0	0	N
8/14	2	0.8	0	0	-	-	-	-	0.01	F
8/28	5	0.8	0.07	0.03	-	-	-	-	0.02	N
9/11	15	0.8	0.16	0.04	-	-	-	-	0.04	F
9/25	2	0.8	0.07	0.05	-	-	-	-	0.01	N
10/9	2	0.9	0.07	0.05	-	-	-	-	0	F
10/23	0	0	0	0	0	0	0	0	0	N
11/5	3	0.7	0.15	0.09	-	-	-	-	0.01	F
11/17	0	0	0	0	0	0	0	0	0	N

Table 19

Ghost Crab Census

Transect 1 1982

PRIMARY

Date	B	MS	SD	SE	MD	N*	SD	SE	SM	MF
4/13	0	0	0	0	0	0	0	0	0	F
4/23	0	0	0	0	0	0	0	0	0	N
5/7	4	1.7	1.24	0.62	59.0	1	0	0	0.05	F
5/21	22	1.9	1.07	0.23	50.8	12	15.01	4.33	0.31	N
6/4					LOST BAD WEATHER					F
6/18	14	2.3	1.36	0.36	32.6	11	8.44	2.55	0.26	N
7/2	8	1.8	1.23	0.44	47.0	3	15.52	8.96	0.13	F
7/17	16	2.8	1.27	0.32	48.7	12	21.50	6.21	0.18	N
8/6	21	2.4	1.09	0.24	43.7	21	26.87	5.86	0.26	F
8/20	39	2.3	1.16	0.19	57.1	31	36.56	6.57	0.48	N
9/3	33	1.6	0.97	0.17	52.2	16	25.68	6.42	0.41	F
9/17	18	1.0	0.88	0.21	-	-	-	-	0.33	N
10/1	20	1.6	1.12	0.25	85.5	6	37.67	15.38	0.44	F
10/15	25	1.1	0.45	0.09	64.7	6	32.49	13.26	0.69	N
10/29	10	1.0	0.16	0.05	65.5	2	27.58	19.50	0.14	F
11/12	0	0	0	0	0	0	0	0	0	N

B, Number of Burrows; MS, Mean Size (Dia.); MD, Mean Depth;
SM, Number Per Square Meter; MF, Moon Phase
* Number used to calculate Mean Depth
\- No depth values taken burrows under 1.0 cm in diameter

Table 19 (cont'd.)

SECONDARY

Date	B	MS	SD	SE	MD	N*	SD	SE	SM	MF
4/13	0	0	0	0	0	0	0	0	0	F
4/23	0	0	0	0	0	0	0	0	0	N
5/7	1	2.0	0.00	0.00	54.0	1	0	0	0.01	F
5/21	14	1.7	1.07	0.29	34.5	8	16.72	5.91	0.19	N
6/4					LOST BAD WEATHER					F
6/18	14	2.5	1.26	0.34	42.0	12	17.70	5.11	0.26	N
7/2	10	2.3	1.76	0.56	41.5	6	12.05	4.92	0.16	F
7/17	32	2.8	1.47	0.26	48.5	28	19.63	3.71	0.36	N
8/6	22	2.3	0.91	0.19	43.0	20	20.80	4.65	0.27	F
8/20	30	2.3	1.29	0.24	60.0	22	34.22	7.30	0.37	N
9/3	40	1.6	1.43	0.23	56.1	12	23.93	6.91	0.49	F
9/17	9	0.8	0.26	0.09	-	-	-	-	0.25	N
10/1	15	1.1	0.56	0.15	100.5	2	47.38	33.50	0.33	F
10/15	21	1.1	0.34	0.08	40.3	4	5.68	2.84	0.58	N
10/29	6	0.9	0.13	0.05	-	-	-	-	0.08	F
11/12	0	0	0	0	0	0	0	0	0	N

Table 19 (cont'd.)

COMBINED

Date	B	MS	SD	SE	MD	N*	SD	SE	SM	MF
4/13	0	0	0	0	0	0	0	0	0	F
4/23	0	0	0	0	0	0	0	0	0	N
5/7	5	1.7	1.08	0.49	56.5	2	3.54	2.50	0.03	F
5/21	36	1.8	1.06	0.18	44.3	20	17.35	3.88	0.25	N
6/4					LOST BAD WEATHER					F
6/18	28	2.4	1.29	0.24	37.5	23	14.56	3.04	0.26	N
7/2	18	2.1	1.54	0.36	43.3	9	12.59	4.20	0.14	F
7/17	48	2.8	1.40	0.20	48.6	40	19.93	3.15	0.27	N
8/6	43	2.3	0.99	0.15	43.3	41	23.80	3.72	0.27	F
8/20	69	2.3	1.21	0.15	58.3	53	35.30	4.85	0.43	N
9/3	73	1.6	1.24	0.14	53.8	28	24.57	4.64	0.45	F
9/17	27	0.9	0.73	0.14	-	-	-	-	0.30	N
10/1	35	1.4	0.94	0.16	89.3	8	37.18	13.14	0.39	F
10/15	46	1.1	0.40	0.06	54.9	10	27.50	8.70	0.64	N
10/29	16	1.0	0.15	0.04	65.5	2	25.58	19.50	0.11	F
11/12	0	0	0	0	0	0	0	0	0	N

Table 20

Ghost Crab Census

Transect 2 1982

PRIMARY

Date	B	MS	SD	SE	MD	N*	SD	SE	SM	MF
4/17	0	0	0	0	0	0	0	0	0	F
4/23	0	0	0	0	0	0	0	0	0	N
5/7	2	0.9	0.14	0.10	0	0	0	0	0.01	F
5/21	13	2.3	0.94	0.26	56.3	11	17.07	5.15	0.08	N
6/4					LOST BAD WEATHER					
6/18	13	2.3	0.80	0.22	43.7	11	18.55	5.59	0.10	N
7/2	10	3.0	0.99	0.31	48.9	10	10.26	3.24	0.08	F
7/17	4	1.9	0.51	0.25	61.8	4	17.46	8.73	0.04	N
8/6	2	3.3	0.42	0.30	55.0	2	7.07	5.00	0.02	F
8/20	15	2.2	0.98	0.25	75.1	13	27.61	7.66	0.11	N
9/3					LOST CAMPER					F
9/17	58	0.8	0.20	0.03	19.0	2	15.56	11.00	0.59	N
10/1	21	1.2	0.77	0.17	42.5	4	34.02	17.01	0.21	F
10/15	21	0.9	0.19	0.04	33.0	3	10.58	6.11	0.21	N
10/29	35	0.9	0.16	0.03	22.5	2	0.71	0.50	0.39	F
11/12	0	0	0	0	0	0	0	0	0	N

B, Number of Burrows; MS, Mean Size (Dia.); MD, Mean Depth;
SM, Number Per Square Meter; MF, Moon Phase
* Number used to calculate Mean Depth
\- No depth values taken burrows under 1.0 cm in diameter

Table 20 (cont'd.)

SECONDARY

Date	B	MS	SD	SE	MD	N*	SD	SE	SM	MF
4/13	0	0	0	0	0	0	0	0	0	F
4/23	0	0	0	0	0	0	0	0	0	N
5/7	2	3.1	0.64	0.45	26.0	2	14.14	10.00	0.01	F
5/21	17	2.0	1.17	0.28	50.7	13	15.17	4.21	0.10	N
6/4				LOST BAD WEATHER						F
6/18	13	2.3	1.15	0.32	45.2	9	18.85	6.28	0.10	N
7/2	8	2.8	1.33	0.47	51.0	6	11.75	4.80	0.06	F
7/17	7	2.0	0.81	0.30	50.9	7	23.93	9.05	0.06	N
8/6	3	2.8	0.76	0.44	62.7	3	34.93	20.17	0.03	F
8/20	14	2.0	1.30	0.35	72.8	9	23.92	7.97	0.10	N
9/3	27	1.2	1.04	0.20	95.8	5	29.81	13.33	0.23	F
9/17	56	0.9	0.40	0.05	67.3	4	25.91	12.96	0.62	N
10/1	19	1.3	0.65	0.15	45.3	7	19.78	7.48	0.19	F
10/15	9	1.0	0.14	0.05	26.0	2	16.97	12.00	0.09	N
10/29	24	0.9	0.21	0.04	45.3	3	18.72	10.81	0.27	F
11/12	0	0	0	0	0	0	0	0	0	N

Table 20 (cont'd.)

COMBINED

	B	MS	SD	SE	MD	N*	SD	SE	SM	MF
4/13	0	0	0	0	0	0	0	0	0	F
4/23	0	0	0	0	0	0	0	0	0	N
5/7	4	2.0	1.30	0.65	26.0	2	14.14	10.00	0.01	F
5/21	30	2.1	1.07	0.19	53.3	24	15.96	30.26	0.09	N
6/4					LOST BAD WEATHER					F
6/18	26	2.3	0.97	0.19	44.4	20	18.20	4.07	0.10	N
7/2	18	2.9	1.12	0.26	49.7	16	10.50	2.62	0.07	F
7/17	11	1.9	0.68	0.21	54.8	11	21.57	6.50	0.05	N
8/6	5	3.0	0.64	0.28	55.8	5	24.96	11.16	0.02	F
8/20	29	2.1	1.13	0.21	74.1	22	25.59	5.46	0.11	N
9/3	27	1.2	1.04	0.02	95.8	5	29.81	13.33	0.23	F
9/17	114	0.8	0.32	0.03	51.2	6	32.74	13.37	0.60	N
10/1	40	1.2	0.70	0.11	44.3	11	24.17	7.29	0.20	F
10/15	30	0.9	0.18	0.03	30.2	5	11.95	5.34	0.15	N
10/29	59	0.9	0.18	0.02	36.2	5	18.21	8.14	0.33	F
11/12	0	0	0	0	0	0	0	0	0	N

Table 21

Ghost Crab Census

Transect 3 1982

PRIMARY

Date	B	MS	SD	SE	MD	N*	SD	SE	SM	MF
4/13	0	0	0	0	0	0	0	0	0	F
4/23	0	0	0	0	0	0	0	0	0	N
5/7	0	0	0	0	0	0	0	0	0	F
5/21	0	0	0	0	0	0	0	0	0	N
6/4					LOST BAD WEATHER					F
6/18	1	1.1	0	0	5.0	1	0	0	0.01	N
7/2	0	0	0	0	0	0	0	0	0	F
7/17	0	0	0	0	0	0	0	0	0	N
8/6	0	0	0	0	0	0	0	0	0	F
8/20	4	0.8	0.15	0.08	-	-	-	-	0.02	N
9/3	6	0.8	0.15	0.06	-	-	-	-	0.03	F
9/17	4	0.8	0.10	0.05	-	-	-	-	0.02	N
10/1	6	0.9	0.11	0.04	-	-	-	-	0.04	F
10/15	5	1.0	0.15	0.07	21.0	1	0.00	0.00	0.04	N
10/29	1	0.9	0.00	0.00	-	-	-	-	0.01	F
11/12	0	0	0	0	0	0	0	0	0	N

B, Number of Burrows; MS, MeanSize (Dia.); MD, Mean Depth;
SM, Number Per Square Meter; MF, Moon Phase
* Number used to calculate Mean Depth
\- No depth values taken burrows under 1.0 cm in diameter

Table 21 (cont'd.)

SECONDARY

Date	B	MS	SD	SE	MD	N*	SD	SE	SM	MF
4/13	0	0	0	0	0	0	0	0	0	F
4/23	0	0	0	0	0	0	0	0	0	N
5/7	0	0	0	0	0	0	0	0	0	F
5/21	1	2.4	0	0	57.0	1	0	0	0.01	N
6/4					LOST BAD WEATHER					F
6/18	0	0	0	0	0	0	0	0	0	N
7/2	0	0	0	0	0	0	0	0	0	F
7/17	0	0	0	0	0	0	0	0	0	N
8/6	0	0	0	0	0	0	0	0	0	F
8/20	1	0.7	0.00	0.00	-	-	-	-	0.00	N
9/3	5	0.6	0.11	0.05	-	-	-	-	0.02	F
9/17	13	0.8	0.13	0.04	-	-	-	-	0.07	N
10/1	3	1.0	0.12	0.07	28	1	0.00	0.00	0.02	F
10/15	2	1.0	0.07	0.05	-	-	-	-	0.01	N
10/29	3	0.6	0.12	0.07	-	-	-	-	0.02	F
11/12	0	0	0	0	0	0	0	0	0	N

Table 21 (cont'd.)

COMBINED

Date	B	MS	SD	SE	MD	N*	SD	SE	SM	MF
4/13	0	0	0	0	0	0	0	0	0	F
4/23	0	0	0	0	0	0	0	0	0	N
5/7	0	0	0	0	0	0	0	0	0	F
5/21	1	2.4	0	0	57.0	1	0	0	0.00	N
6/4					LOST BAD WEATHER					F
6/18	1	1.1	0	0	5.0	0	0	0	0.00	N
7/2	0	0	0	0	0	0	0	0	0	F
7/17	0	0	0	0	0	0	0	0	0	N
8/6	0	0	0	0	0	0	0	0	0	F
8/20	5	0.8	0.14	0.06	-	-	-	-	0.01	N
9/3	11	0.7	0.16	0.05	-	-	-	-	0.03	F
9/17	17	0.8	0.12	0.03	-	-	-	-	0.05	N
10/1	9	0.9	0.11	0.04	28	1	0.00	0.00	0.03	F
10/15	7	1.0	0.13	0.05	21.0	1	0.00	0.00	0.03	N
10/29	4	0.7	0.16	0.08	-	-	-	-	0.02	F
11/12	0	0	0	0	0	0	0	0	0	N

LIST OF REFERENCES

LIST OF REFERENCES

Alexander, H.G.L. 1979. A preliminary assessment of the role of terrestrial decapod crustaceans in the Aldabran ecosystem. Phil. Trans. R. Soc. Lond. B. 286: 241-246.

Anders, F.J. and S.P. Leatherman. 1981. The effects of off-road vehicles on beach and dune systems Fire Island National Seashore, Final Report. University of Massachusetts, Amherst, National Park Service Cooperative Research Unit Report, No. 50, 176 pp.

Bartberger, Charles E. 1973. Origin, distribution and rates of accumulation of sediments in Chincoteague Bay, Maryland and Virginia. Masters Thesis, Syracuse University. 168 pp.

Bliss, D.E. 1963. The pericardial sacs of terrestrial Brachyura. Pages 59-78. In: H.B. Whittington and W.D.I. Rolfe (Eds.), Phylogeny and Evolution of Crustacea, Museum of Comparative Zoology, Special Publication, Cambridge, Mass. xii + 192 pp.

Britton, E.E. 1979. Evaluation of public use impacts upon nesting shorebirds and the beach habitat on Chincoteague National Wildlife Refuge. Chincoteague National Wildlife Refuge, Chincoteague, Virginia. U.S. Fish and Wildlife Service. 37 pp.

Brodhead, J.M.B. and P.J. Godfrey. 1979. The effects of offroad vehicles on coastal vegetation in the Province Lands, Cape Cod National Seashore, Massachusetts, Final Report. University of Massachusetts, Amherst, National Park Service Cooperative Research Unit Report, No. 32, 240 pp.

Brooke, M. de L.. 1981. Size as a factor influencing the ownership of copulation burrows by the ghost crab (Ocypode ceratophthalmus). Z. Tierpsychol. 55: 63-78.

Bumpus, D.F. 1973. A description of the circulation on the continental shelf of the east coast of the United States. Progr. Oceanogr. 6:111-157.

Byrne, R.J., C. H. Hobbs and M.J. Carron. 1982. Baseline sediment studies to determine distribution, physical properties, sedimentation budgets and rates in the Virginia portion of the Chesapeake Bay, Final Report. Virginia Institute of Marine Science, Gloucester Point, Virginia, 155 pp.

Chakrabarti, A. 1980. Influence of biogenic activity of ghost crabs on the size parameters of beach sediments. Senckenbergiana Marit. 12(5/6):183-199.

Chakrabarti, A. 1981. Burrow patterns of *Ocypode ceratophthalma* (Pallas) and their environmental significance. J. Paleontol. 55(2): 431-511.

Chance, F.A. and H.H. Hobbs. 1969. The freshwater and terrestrial decapod crustaceans of the West Indies with special references to Dominica. Bull. U.S. Nat. Mus. No. 292: 1-258.

Costlow, J.D., and E. Fagetti. 1967. The larval development of the crab, *Cyclograpus cinereus* Dana, under laboratory conditions. Pac. Sci. 21: 166-177.

Coues, E. 1871. Notes on the natural history of Fort Macon, N.C. and vicinity. (No. 2). Proc. Acad. Natur. Sci. of Phila. 23(1): 120-223.

Cowles, R.P. 1908. Habitats, reactions, and associations in *Ocypode arenaria*. Pap. Tortugas Lab. Carnegie Inst. Wash. 2: 1-41.

Crane, J. 1941. Eastern Pacific expeditions of the New York Zoological Society. XXIX. On the growth and ecology of brachyuran crabs of the genus *Ocypode*. Zoologica New York, 26: 297-310.

Diaz, H. and J.D. Costlow. 1972. Larval development of *Ocypode quadrata* (Brachyura: Crustacea) under laboratory conditions. Mar. Biol. 15: 120-131.

Diaz, H. 1974. Life history pattern and population growth of the mole crab *Emerita talpoida* Say. Ph.D. Dissertation, Duke University, 148 pp.

Dolan,R., B. Hayden, and J. Heywood. 1977. Atlas of Environmental Dynamics Assateague Island National Seashore: Natural Resources Report No. 11, National Park Service and National Aeronautics and Space Administration. 40 pp.

Dolan, R., H. Lins and J. Stewart. 1980. Geographical atlas of Fenwick Island, Maryland, a middle Atlantic coast barrier island, Geological Survey Professional Paper 1177-A, U.S. Department of the Interior. 24 pp.

Edney, E.B. 1960. Terrestrial Adaptations. Pages 367-393 in T.H. Waterman (Ed.). The Physiology of Crustacea, Vol. 1. Academic Press, New York and London, xviii + 670 pp.

Efford, I.E. 1970. Recruitment to sedentary marine populations as examplified by the sand crab *Emerita analoga* (Decapoda, Hippidae). Crustaceana 18(3): 293-308.

Efford, I.E. 1976. Distribution of the sand crabs in the genus *Emerita* (Decapoda, Hippidae). Crustaceana 30(2): 169-183.

Fales, R.R. 1976. Apparent predation on the mole crab *Emerita talpoida* (Say) by the ghost crab *Ocypode quadrata* (Fabricius). Ches. Sci., 17(1): 65.

Fellows, D.P. 1973. Behavioral ecology of the ghost crab *Ocypode ceratophthalmus* and *Ocypode cordimana* at Fanning Atoll, Line Island. Pages 219-241. *In*: K.E. Chave and E. Alison Kay, principal investigators. Fanning Island Expedition, July and August, 1972. HIG-73-13. University of Hawaii, Hawaii Institute of Geophysics, Honolulu. iv + 320 pp. (Cited in Vannini, 1980).

Fellows, D.P. 1975. On the distribution of the Hawaiian ghost crab, *Ocypode laevis* Dana. Pac. Sci., Vol. 29: 257-258.

Fisher, J. Berton and Michael J.S. Tevesz. 1979. Within-habitat spatial patterns of *Ocypode quadrata* (Fabricius) (Decapoda Brachyura). Crustaceana, Suppl. 5, 31-36 pp.

Ford, W.L. and A.R. Miller. 1952. The surface layer of the Gulf Stream and adjacent waters. J. Mar. Res. 11: 267-280.

Forschuts, O. and N.F. Williams. 1978. Public and wildlife use on beaches of Pea Island National Wildlife Refuge, Washington, D.C. U.S. Fish and Wildlife Service. 29 pp.

Fusaro. C. 1978. Growth rate of the sand crab, *Emerita analoga*, (Hippidae) in two different environments. Fish. Bull. 76(2): 369-375.

Grant, D. 1983. Ghost crabs at Sandy Hook, NJ. Underwater Naturalist. 14(3):25.

Grant, G.C. 1979. Middle Atlantic bight zooplankton: Second year results and a discussion of the two-year BLM-VIMS surveys. Chapter 4 *in* Middle Atlantic Outer Continental Shelf Environmental Studies. Virginia Institute of Marine Science. Special Report in Applied Marine Science and Ocean Engineering. No. 192. 236 pp.

Gross, G.M. 1972. Oceanography, a view of the earth. Prentice-Hall, Inc. New Jersey. 581 pp.

Haley, S.R. 1969. Relative growth and sexual maturity of the Texas ghost crab, *Ocypode quadrata* (Fabr.) (Brachyura, Ocypodidae). Crustaceana, 19(3): 285-297.

Haley, S.R. 1972. Reproductive cycling in the ghost crab, *Ocypode quadrata* (Fabr.) (Brachyura, Ocypodidae). Crustaceana 23(1): 1-11.

Hanson, A.J. 1969. The larval development of the sand crab *Hippa cubensis* (De Saussure) in the laboratory (Decapoda, Anomura), Crustaceana, 16(2): 143-157.

Hedgpeth, J.W. 1957. Sandy Beaches. Pages 587-608. *In*: Treatise on marine ecology and palaecology, Volume 1, Ecology. Ed. J.W. Hedgpeth. Geol. Soc. Am. Mem. 67. vii + 1296 pp.

Hill, G.W. and R.E. Hunter. 1973. Burrows of the ghost crab *Ocypode quadrata* (Fabricius) on the barrier islands, south-central Texas coast. J. Sed. Petrology. 43(1): 24-30.

Horch, K. 1971. An organ for hearing and vibration sense in the ghost crab *Ocypode*. Zeitschr. vergl. Physiol., 73: 1-21.

Horch, K. 1974. Barth's myochordotonal organ as an acoustic sensor in *Ocypode*. Experienta, 30(6): 630-631.

Horch, K. 1975. The acoustic behavior of the ghost crab *Ocypode cordimana* Latreille, 1818 (Decapoda, Brachyura) Crustaceana. 29(2): 193-205.

Horch, K.W. and M. Salmon. 1969. Production, perception and reception of acoustic stimuli by semiterrestrial crabs (Genus *Ocypode* and *Uca*, Family *Ocypodidae*). Forma Functio. 1: 1-25.

Horch, K.W. and M. Salmon. 1972. Responses of the ghost crab, *Ocypode* to acoustic stimuli. Zeitschr. Tierpsychol., 30: 1-13.

Hughes, D.A. 1966. Behavioral and ecological investigations of the crab *Ocypode ceratophthalmus* (Crustacea: Ocypodidae) J. Zool., Lond. 150: 129-143.

Hughes, D.A. 1973. On mating and the "Copulation Burrows" of crabs of the genus *Ocypode* (Decapoda, Brachyura). Crustaceana 24(1): 72-76.

Ingham, M.C. Editor. 1982. Summary of the physical oceanographic processes and features pertinent to pollution distribution in the coastal and offshore waters of the Northeastern United States, Virginia to Maine. NOAA Technical Memorandum NMFS-F/NEC-17. 166 pp.

Jones, A.C., D.E. Dimitriou, J.T. Ewald, and J.H. Tweedy. 1970. Distribution of early developmental stages of pink shrimp, *Penaeus duorarum*, in Florida waters. Bull. Mar. Sci. 20(3): 634-661.

Jones, D.A. 1972. Aspects of the ecology and behaviour of *Ocypode ceratophthalmus* (Pallas) and *O. kuhlii* de Haan (Crustacea: Ocypodidae). J. Exp. Mar. Biol. Ecol. 8: 31-43.

Leber, K.M. 1981. Spatial Patterns of *Ocypode quadrata*: re-evaluation (Decopoda, Brachyura), Crustaceana, 41(1): 110-112.

Lee, T.N. 1975. Florida current spin-off eddies. Deep-sea Res. Oceanogr. Abstract. 22: 753-765.

Leggett, A. Thomas. 1975. A population and behavioral study of the ghost crab, *Ocypode quadrata* (Fab.) at the Back Bay National Wildlife Refuge: A continuation. Old Dominion University, Va. Department of Biological Sciences (Unpublished Report). 47 pp.

Leggett, A. Thomas, Jr. and Gary Lee Butler. 1975. Preliminary rpt. on a population and behavior of the ghost crab *Ocypode quadrata* (Fab.) at the Back Bay WildLife Refuge. Old Dominion University, Va. Department of Biological Sciences (Unpublished Report). 18 pp.

Letterman, G.R. 1973. Natural history of *Ocypode quadrata* with comparative investigations of *Ocypode ceratophthalma* and *Ocypode cordimana*. Masters Thesis, *University of Delaware, Newark, Delaware.* 107 pp.

Liddle, M.J. and P. Greig-Smith. 1975. A survey of tracks and paths in a sand dune ecosystem, II. Vegetation. J. Appl. Ecol. 12(3):909-930.

Lighter, F.J. 1974. A note on a behavioral spacing mechanism of the ghost crab *Ocypode geratophthalmus* (Pallas) (Decapoda, family Ocypodidae). Crustaceana 27(3): 312-314.

Linsenmair, K.E. 1965. Optische signalisierung der kopulatlonshohle bei der reiterkabbe *Ocypode saratan* forsk (Decapoda Brachyura Ocypodidae). Naturwissenchaften 52: 256-257. (Cited in Hughes, 1973).

Linsenmair, K.E. 1967. Konstruktion und signalfunktion der sandpyramide der retericrabbe *Ocypode saratan* forsk (Decapoda Brachyura Ocypodidae). Zeitschr. Tierpsychol., 24: 403-456. (Cited in Hughes, 1973 and Vannini, 1980).

McDowall, R.M. 1969. Lunar rhythms in aquatic animals, a general review. Tuatara 17(3):133-144.

McLachlan, A. 1980. Occurrence of ghost crabs *Ocypode* spp., in the eastern Cape. S. Afr. J. Zool. 15 (1): 57-58.

Messeri, P. 1978. Some observations on a littoral troop of yellow baboons. Monitore Zool. Ital. (N.S.) 12:69. (Cited in Vannini, 1980).

Millikin, Mark R. and Austin B. Williams. 1984. Synopsis of biological data on the blue crab, *Callinectes sapidus* Rathbun. U.S. Dept. Commer., NOAA Tech. Rpt. NMFS 1, 39 pp.

Milne, L.J. and Margery J. Milne. 1946. Notes on the behavior of the ghost crab. Amer. Nat. 80(792): 362-380.

Nagabhushanam, R., and K.R. Rao. 1967. Studies on the moult cycle in the crab, Ocypode macrocera. In Proceedings of the Symposium on Crustacea, Part III, Marine Biological Association of India. 1099-1107.

Paulraj, S., Mullainadhan, P., & Ravindranath, M.H. 1982. Relative growth before and after sexual maturity in Ocypode platytarsis (Milne Edwards) and Ocypode cordimana (Desmarest) (Crustacea: Decapoda). Intl. J. Invert. Reprod. 5: 115-128.

Phillips, A.M. 1940. The ghost crab. Natur. Histor., Vol. XLVI: 36-41.

Phillips, P.J., W.D. Burke and E.J. Keener. 1969. Observations on the trophic significance of jellyfish in Mississippi Sound with quantitative data on the associated behavior of small fish with medusae. Trans. Amer. Fish. Soc. 98(4): 703-712.

Rao, K. Ranga. 1966. Studies on the influence of environmental factors on growth in the crab, Ocypode macrocera H. Milne Edwards. Crustaceana, 11, Pt. 3: 257-276.

Rao, K.R. 1968. The pericardial sacs of Ocypode in relation to the conservation of water, moulting, and behavior. Amer. Zool. 8(3): 561-567.

Rathbun, M.J. 1918. The Grapsoid Crabs of America. Bull. U.S. Nat. Mus. 97: 1-145.

Rees, G.H. 1959. Larval development of the sand crab Emerita talpoida (Say) in the laboratory. Biol. Bull., 117:(2): 356-370.

Robertson, J. Roy and William J. Pfeiffer. 1981. Deposit-feeding by the ghost crab Ocypode quadrata (Fabricius). J. Exp. Mar. Biol. Ecol.d 56: 165-177.

Sandifer, P.A. 1973. Distribution and abundance of decapod crustacean larvae in the York River estuary and adjacent lower Chesapeake Bay, Virginia, 1968-1969. Ches. Sci. 14(4): 235-257.

Scheltema, Rudolf S. 1975. Relationship of larval dispersal, gene-flow and natural selection to geographic variation of benthic invertebrates in estuaries and along coastal regions. In: Estuarine Research, Vol. 1, Chemistry, Biology and the Estuarine System. Ed. L. Eugene Cronin. Academic Press, Inc. xiv + 738 pp.

Schone, H. 1968. Agonistic and sexual display in aquatic and semi-terrestrial Brachyuran crabs. Amer. Zool. 8: 641-654.

Sigrist, P.E. Soil limitations on Assateague Island. Soil Conservation Service and Worcester Soil Conservation District. U.S. Department of Agriculture. 26 pp.

Smith, D.E. and Jack W. Jossi. 1984. Net phytoplankton and zooplankton in the New York Bight, January 1976 to February 1978, with comments on the effects of wind, Gulf Stream eddies, and slope water intrusions. NOAA Technical Report NMFS 5, 8 pp.

Smith, S.I. 1873a. The megalops stage of Ocypoda. Amer. J. of Sci. and Arts, Series 3, 6(31): 67-68.

Smith, S.I. 1873b. C. - The metamorphoses of the lobster, and other Crustacea. Pages 522-537. In: A.E. Verrill, Report upon the invertebrate animals of Vineyard Sound and adjacent waters, with an account of the physical characters of the Region, pages 295-778, Plates 1-38. In: Spencer F. Baird, Report on the condition of the sea fisheries of the south coast of New England in 1871 and 1872. United States Commission of Fish and Fisheries, 1:XLVII + 852 pp.

Smith, S.I. 1880. Occasional occurrence of tropical and sub-tropical species of decapod Crustacea on the coast of New England. Trans. Conn. Acad. Arts and Sci., 4(6): 254-267.

Smith, T.J. 1978. Public and wildlife use on beaches of Pea Island National Wildlife Refuge: Addendum to the Final Report Asheville, N.C. U.S. Fish and Wildlife Service. 4 pp.

Sokal, R.P., and F.J. Rohlf. 1981. Biometry, The principles and practices of statistics in biological research. W.H. Freeman and Company, San Francisco. 859 pp.

Steiner, A. and Leatherman, S.P. 1979. A preliminary study of the environmental effects of recreational usage on dune and beach ecosystems of Assateague Island. National Park Service Cooperative Research Unit Report Number 44. Univ. of Massachusetts. 101 pp.

Steiner, Alan J. & Stephen P. Leatherman. 1981. Recreational impacts on the distribution of ghost crabs (Ocypode quadrata fab). Biol. Conserv., 20: 111-122.

Stephens, W.M. 1965. Land crabs. Sea Frontiers 11(4): 194-201.

Takahasi, S. 1932. On the burrows of Ocypoda ceratophthalma Fabricius. Kwagaka-Tisiki, 2: 329-335.

Teerling, J. 1970. The incidence of the ghost crab Ocypode quadrata (Fabr) on the forebeach of Padre Island, and of its responses to man. Unpublished, Masters Thesis. Texas A and I University. Kingsville, Texas. 71 pp.

Trew, M.J. 1973. The effects and management of trampling on coastal sand dunes. J. Env. Plan. and Pol. Cont. 1(4):38-49.

Trott, T.J. and J.R. Robertson. 1984. Chemical stimulants of cheliped flexion behavior by the western Atlantic ghost crab Ocypode quadrata (Fabricius). J. Exp. Mar. Biol. Ecol., 78: 237-252.

Tweedie, M.W.F. 1950. Notes on grapsoid crabs from the Raffle Museum. Bull. Raffles Mus. 23: 310-324.

U.S. Department of Commerce, NOAA, NOS. 1980. Tide Tables 1981 - High and Low Water Predictions, East Coast of North and South America, including Greenland. 285 pp.

U.S. Department of Commerce, NOAA, NOS. 1981. Tide Tables 1981 - High and Low Water Predictions, East Coast of North and South America, including Greenland. 285 pp.

U.S. Department of the Interior. 1982. National Park Service, General Management Plan - Assateague Island National Seashore. 93 pp.

U.S. Environmental Protection Agency. Draft Environmental Impact Statement, North-Central Ocean Basin Regional Wastewater Treatment Facility, Worcester County, Maryland. Region III. 1977. Philadelphia, PA. 216 pp.

Vader, Wm. 1982. Pied wagtails catching young ghost crabs. Ostrich. 53(4): 205.

Vannini, M. 1980. Researches on the coast of Somalia. The shore and the dune of Sar Uanle. 27. Burrows and digging behaviour in Ocypode and other crabs (Crustacea Brachyura). Monitore Zoologico Italiano (N.S.) Suppl. 13: 12-44.

Warburg, M.R. and E. Shuchman. 1979. Experimental studies on burrowing of Ocypode cursor (L.) (Crustacea; Ocypodidae), in response to sand-moisture. Mar. Behav. Physiol. 6: 147-156.

Wesche, A. Personal communication. Maryland Department of Natural Resources, West Ocean City, Maryland, 1980.

Wharton, G.W. 1942. A typical sand beach animal, the mole crab, Emerita talpoida (Say). In: Pearce, Humm, and Wharton, Ecology of sand beaches at Beaufort, N.C. Ecol. Monogr., 12(2): 35-190.

Williams, A.B. 1974. The swimming crabs of the genus Callinectes (Decapoda: Portunidae). Fish. Bull., 72(3): 685-798.

Williams, A.B. 1984. Shrimps, lobsters, and crabs of the Atlantic Coast of the Eastern United States, Maine to Florida, Smithsonian Institution Press, Washington, D.C. 550 pp.

Wolcott, T.G. 1976. Uptake of soil capillary water by ghost crabs. Nature. 264 (5588): 756-757.

Wolcott, T.G. 1978. Ecological role of ghost crabs, *Ocypode quadrata* (Fabricius) on an ocean beach: scavengers or predators? *J. Exp. Mar. Biol. Ecol.* 31: 67-82.

Wolcott, T. G. 1984. Uptake of interstitial water from soil: mechanisms and ecological significance in the ghost crab *Ocypode quadrata* and two Gecarcinid land crabs. Physiol. Zool. *57(1): 161-184.*

Wolcott, T.G. and D.L. Wolcott. 1982. Larval loss and spawning behavior in the land crab *Gecarcinus lateralls* (Freminville). J. Crust. Biol. *2(4): 477-485.*

Wright, Howard O. 1968. Visual displays in Brachyuran crabs: Field and laboratory studies. Amer. Zool. 8: 655-665.

Zaremba, R.E., P.J. Godfrey and S.P. Leatherman. 1979. The ecological effects of off-road vehicles on the beach/backshore (drift line) zone in Cape Cod National Seashore, Massachusetts. University of Massachusetts, Amherst, National Parks Service Cooperative Research Unit, Report No. 29, 67 pp.