BEHAVIOURAL ECOLOGY OF CRABS IN TEMPERATE MANGROVE SWAMPS

JANICE H. WARREN

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The work contained in this thesis, except where otherwise acknowledged, is the result of my own investigations.

Signed: [redacted]

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SUMMARY

Patterns of distribution of crabs inhabiting burrows in three temperate mangrove swamps near Sydney, New South Wales, were described. Heloecius cordiformis (an ocypodid) did not exhibit a consistent pattern of distribution among three tidal zones, but was always associated with well-drained mounds of substratum within zones. Paragrapsus laevis (a grapsid) tended to be most abundant in the lower two zones on the shore and usually inhabited burrows in the moist or submerged flats between mounds. Sesarma erythrodactyla (a grapsid) was distributed fairly evenly among the three tidal zones and also between mounds and flats. H. cordiformis hibernated in burrows from June through August or September. Overall abundances also varied seasonally, but trends were inconsistent among the three swamps sampled.

The sizes of males and females were similar for each species. H. cordiformis, however, tended to be larger higher on the shore. Sex ratios were inconsistent for P. laevis and S. erythrodactyla, but female H. cordiformis usually outnumbered males.

The seasonal timing of ovigery for each species differed. The greatest proportions of ovigerous females were found in autumn for H. cordiformis, in winter for P. laevis, and in summer for S. erythrodactyla.

Habitat selection (preference) and interspecific interactions were two mechanisms tested to explain the distributions of species between two microhabitats - mounds and flats. Experiments revealed that the observed

distributional patterns were largely the result of choice and that the presence of other species in experimental enclosures had little effect on where crabs settled (i.e. where crabs and burrows were found).

Habitat selection was influenced by topography and by the sediments associated with each microhabitat. H. cordiformis, for example, preferred mounds to flats but only if the mounds were undisturbed or composed of disturbed mound material; experimental mounds of disturbed material from flats were avoided. Provision of artificial burrows in mounds or flats made these more attractive to P. laevis and S. erythrodactyla (which cannot construct proper burrows). H. cordiformis, however, still preferred mounds, even when artificial burrows were provided only in flats.

Because H. cordiformis deposit material excavated from burrows adjacent to the entrance at the surface, these crabs might be responsible for the presence of mounds in mangrove swamps. This model was tested by enclosing crabs in initially flat areas of the swamp and measuring the topographic complexity after two weeks and after four months. Areas subject to burrowing by crabs had greater relief (i.e. a 'moundier' topography) than control areas without crabs.

Another significant effect of H. cordiformis on the substratum was skewing of the distribution of grain-sizes toward coarser sands rather than the fine silts and clays that characterise the sediments in flats. This resulted from crabs burrowing into the coarser sediments beneath the surface and depositing this material onto the surface. Although the concentrations

of organic material were similar in areas with or without crabs, microalgal abundance was significantly reduced in areas with crabs.

The spatial and temporal patterns of behaviour of *H. cordiformis* (primarily) and the two grapsid species were examined. All crabs were active on the surface during diurnal periods of emersion, but *P. laevis* and *S. erythrodactyla* were also active at night. Throughout a given period of emersion, neither the numbers of crabs active on the surface nor the nature of behaviours varied significantly among the early, middle and late periods of activity of *H. cordiformis*. For the majority of the time spent on the surface, crabs were engaged in feeding, maintenance of the burrow, forming mud balls to bring down the burrow or pausing at the burrow. Episodes of courtship or agonistic encounters were relatively rare. Males and females exhibited similar behavioural patterns, except that courtship was always initiated by males at a female's burrow.

Most activities were performed at or near the entrances to burrows. The two activities performed furthest from the burrow were forming mud balls (to bring into the burrow) and courtship by males at the burrows of females. Fidelity to burrows was short; most crabs changed burrows within a 48-hr period.

Burrows were very effective at reducing mortality from predation during high tide. Field experiments demonstrated that virtually all crabs remaining on the surface during submersion are likely to be preyed upon by toadfish within the first few hours of tidal inundation.

The behaviour of mangrove crabs largely explains their small-scale spatial and temporal patterns of distribution in mangrove swamps.

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CHAPTER 1. GENERAL INTRODUCTION

Background

Distributional patterns of intertidal organisms on rocky shores have been the subject of numerous investigations. These have focused on patterns of vertical distribution, i.e. zonation (see reviews by Chapman 1973; Connell 1972; Underwood 1979) and patterns of distribution in various microhabitats within zones (e.g. crevices, pools, (Kohn 1983; Levings and Garrity 1983; McGuinness and Underwood 1987; Menge and Lubchenco 1981; Moran 1985). On rocky shores, interactions among several principal mechanisms account for these patterns; these include tolerance to physical and chemical conditions, competition and predation, variations in recruitment and habitat selection (e.g. reviews by Connell 1972; Underwood 1979; Underwood and Denley 1984).

Mechanisms underlying distributional patterns of intertidal invertebrates on soft substrata have been investigated only relatively recently (see reviews by Gray 1974; Peterson 1979; Rhoads 1974; Woodin 1983). Dayton (1984) suggested that the processes affecting distributions on these shores differ from rocky shores, with interspecific competition being less important because the organisms on sandy or muddy shores can penetrate the substratum and thus exploit habitats other than those on the surface.

Studies of intertidal invertebrates on high energy sandy beaches have focused on the effects of rhythmic activity on the maintenance of zonal patterns (e.g. Alheit and Naylor 1976; Ansell and Trevallion 1969; Efford 1965; Enright 1961, 1963; Fish and Fish 1972; Jones and Hobbins 1985; Williams 1979). Similar studies have been done on estuarine shores (e.g.

Barnes 1981, 1986; Dieleman 1979). In this latter environment, however, one group of invertebrates is particularly noticeable, the burrowing crabs.

The two families, Ocypodidae and Grapsidae, contain the vast majority of species in salt marshes, mangrove swamps, and tidal mudflats. The most extensive research has been done for fiddler crabs (genus Uca), especially for species associated with the salt marshes of the southern and eastern shores of the United States (Crane 1975). Eighteen of the 19 genera comprising the Ocypodidae are associated with mangrove swamps worldwide, with Uca contributing the largest number of species (Jones 1984).

In Australia, fiddler crabs are abundant in the tropics and subtropics, but are rare in the temperate swamps of New South Wales. Instead, a close relative, the semaphore crab Heloecius cordiformis (H. Milne Edwards), dominates (Hutchings and Recher 1982). These crabs are behaviourally very similar to the fiddler crabs and, therefore, present an opportunity to compare aspects of their behavioural ecology to those of the better-known Uca species.

Many of the studies of crabs in temperate estuarine habitats in Australia provided only species lists and descriptions of distributional patterns (primarily among zones)(Hutchings and Recher 1974, 1982; Hutchings et al. 1977; McCormick 1978; Snelling 1959). In general, the greatest abundances of most species were found toward the seaward edge of swamps.

Griffin (1968) discussed some of the similarities between H. cordiformis and Uca species but the populations of H. cordiformis that he studied were in estuaries without mangroves in Tasmania (south of mainland Australia). Griffin (1971) also experimentally tested the importance of habitat selection to patterns of distribution of several species on shores with different substrata, and found that preference demonstrated in the laboratory correlated well with natural distributions.

Yates (1978) experimentally determined that habitat selection was important to the establishment of zonal patterns for several species of crabs in a single mangrove swamp north of Sydney. The only other experimental study of temperate mangrove crabs was that of McKillup and Butler (1979) who determined that crabs had behavioural patterns that limited the number of burrows in an area to a density below that which would result in collapse of the substratum.

In mangrove swamps near Sydney, abundances of crabs within zones appear to be very patchy. McCormick (1978) and Yates (1978) suggested that certain species were more abundant in well-drained mounds of substratum whereas others dominated the adjacent moist or submerged flats. Griffin's (1968) behavioural observations of H. cordiformis, the species most abundant in mounds, provided evidence that this species might, in fact, be creating the mounds containing their burrows. When H. cordiformis remove material from burrows, they deposit balls of sediment just outside or near the entrances. The daily contribution of material from a cluster of burrows could easily result in the formation of a mound.

Effects of infauna on the nature of their microhabitats (e.g. topography, distribution of grain-sizes, degree of aeration, etc.) have been demonstrated for a wide range of invertebrates in intertidal and subtidal soft substrata (see reviews by Boucout 1981; Ekdale _et_ _al._ 1984; Rhoads 1974). The burrowing, feeding and other activities of fiddler crabs have also been shown to result in significant bioturbation of the sediments (Allen and Curran 1974; Bell _et_ _al._ 1978; Hoffman _et_ _al._ 1984).

Because _H. cordiformis_ ingest organic matter from sediments, they might substantially reduce algal abundance near their burrows. Dye and Lasiak (1986) and Robertson _et_ _al._ (1980) examined this for fiddler crabs in tropical mangrove swamps and temperate salt marshes, respectively, and found no significant effect but this has never been investigated for _H. cordiformis_.

Spatial and temporal aspects of the behaviour of crabs are clearly important to the distribution, procreation and survival of the species. During the breeding season, for example, reproductive males of several species of fiddler crabs migrate to the landward edge of their salt marsh habitat to construct burrows for mating (Christy and Salmon 1984; Crane 1975; Hyatt and Salmon 1978). Sampling their distributions at this time would provide a very different assessment of their pattern of distribution from that determined from samples taken outside the breeding season. For _H. cordiformis_ (and other species in mangrove swamps near Sydney), the effects of behavioural patterns on distributions, survival, etc., have not yet been examined.

Much of the qualitative work on the behaviour of crabs has provided general descriptions of repertoires and the timing of activities on the surface relative to gross tidal and environmental cycles, e.g activity during diurnal emersion (Crane 1957; Griffin 1965; Ono 1962; Ward 1928). These kinds of studies are an essential first step in the analysis of behaviour because they provide descriptions of activities under natural (field) conditions.

Quantitative behavioural research on crabs and other invertebrates on sandy or muddy shores has been directed toward an understanding of temporal aspects of behaviour, especially with respect to tidal, daily, semilunar and longer environmental periodicities (see revews by DeCoursey 1976, 1983; Naylor and Hartnoll 1979; Palmer 1974). The objective of most of these (predominantly laboratory) studies was to determine whether rhythmic behaviour was controlled by an endogenous 'biological clock'. Research by Enright (1963, 1972), Fish and Fish (1970), Jones and Hobbins (1985), Williams (1969) and many others has usually demonstrated the existence of such a 'clock' in amphipods, isopods, crabs and other invertebrates.

Some quantitative work on behavioural rhythms of crabs has been done in the field. Henmi (1984), Nakasone (1982) and others have compared the numbers of crabs active on the surface among the early, middle and late periods of emersion, and Zucker (1974) determined the proportion of time crabs spent in various activities relative to tidal and daily environmental cycles. Many authors (e.g. Crane 1975; Griffin 1968; Warner 1977) have suggested that crabs progress through a regular sequence of activities during a given period of emersion, but their observations have not been quantified.

Timing of activity on the surface during emersion might provide a temporal refuge from subtidal predators, and most studies of burrowing crabs have suggested that burrows provide a spatial refuge from subtidal, terrestrial or avian predators (Crane 1975; Montague 1980; Warner 1977). None of these investigations has actually tested the effectiveness of the burrow in terms of increased survival. The effectiveness of temporal and spatial refuges on rocky shores has, however, been demonstrated for a variety of gastropods inhabiting home scars or crevices during submergence (when their subtidal predators, primarily fish, are nearby)(Garrity 1984; Garrity and Levings 1983; Levings and Garrity 1983, 1984). Because preliminary observations and analyses of gut contents suggested that toadfish might be important predators of crabs in local mangrove swamps, the role of the burrow as a refuge for crabs against toadfish should be tested.

The Present Study

The initial focus of this study is a description of the distributional patterns of three common species of crabs in three mangrove swamps near Sydney. Previous work indicated that abundances varied among tidal zones, and this was further examined here. In addition, casual observations suggested that within zones these species were probably not randomly distributed with respect to the undulating topography of the substratum. Heloecius cordiformis appeared to be more abundant in mounds; Paragrapsus laevis (Dana) appeared to be more abundant in flats; and Sesarma erythrodactyla Hess was similarly abundant in both microhabitats. Sampling mounds and flats separately within zones, therefore, was done to determine the significance of this smaller-scale pattern of distribution. The prevalence (or persistence) of patterns is discussed with respect to two spatial scales (different areas within zones and three different swamps) and two temporal scales (day-to-day and seasonal differences).

Distributional patterns between microhabitats tended to be far more persistent than differences among tidal zones. One of three mechanisms commonly tested to explain spatial distributions is habitat selection, which proposes that organisms are found in places they choose. An alternative is that interspecific interactions (such as competition, predation or facilitation) underlie patterns of distribution. Both of these mechanisms were investigated here.

A third mechanism that has frequently been tested to explain distributional patterns is tolerance to physical and chemical attributes of a habitat. This was considered irrelevant to the small scale associated with microhabitats in the present study, because crabs could rapidly move the few centimetres necessary to find more suitable conditions.

Because preference was shown to be important during this study, its consequences were investigated in greater detail. The effects of topography, type of material and provision of artificial burrows on distributions between mounds and flats were tested in the field.

For H. cordiformis, the relationship between crabs and the substratum of their habitat was also examined from the perspective of effects crabs have on the substratum. The effects of this species on topography, distribution of grain-sizes (texture), concentration of organic matter and microalgal abundance were tested experimentally.

The final aspect of this study of the behavioural ecology of mangrove crabs was a description of the typical activities of H. cordiformis (the most easily observed species) and an assessment of the proportion of time spent in the various behaviours of their repertoire (frequently called a 'time-budget'). Preference is just one aspect of behaviour important in the explanation of distributional patterns. Other relevant spatial aspects of behaviour were examined, e.g. the frequency of excursions from burrows, distances at which various activities were performed, and the duration of ownership of a particular burrow (fidelity).

Finally, temporal aspects of the behaviour of H. cordiformis are discussed. Previous workers suggested that H. cordiformis and fiddler crabs progress through a regular sequence of behaviours after emergence onto the surface. This was examined for H. cordiformis by analysing differences in the nature of activities from the early to middle and late periods of activity on the surface. In addition, the apparent abundances of all three species were compared between diurnal and nocturnal low tides. These species were active on the surface only during periods of emersion. Because toadfish prey on these species, crabs might be exploiting a temporal refuge by restricting activity on the surface to periods of emersion only. Remaining in burrows during periods of submergence would allow crabs to escape predation by use of these spatial refuges. The effectiveness of burrows as a refuge against subtidal predators was examined by depriving some crabs of burrows during submergence and allowing others to construct and inhabit burrows.

These two areas of research - distributions and behaviour - were designed to contribute to an understanding of the ecology of these dominant members of the macroinvertebrate fauna in mangrove swamps near Sydney. Identification of distributions among zones and microhabitats and subsequent examination of mechanisms underlying these small-scale distributions should greatly increase our knowledge of the patterns and processes important to this special type of soft-sediment community.

CHAPTER 2. STUDY AREAS, SPECIES OF CRABS AND GENERAL METHODS

Sampling of natural populations and experiments were done at three study areas in the Sydney Region of New South Wales: Careel Bay, Woolooware Bay West and Woolooware Bay East (Figure 2.1).

Careel Bay

Careel Bay, the northernmost study area (35 km north of Sydney), is located on the northeastern shore of Pittwater, an inlet which opens northerly into the Hawkesbury River-Broken Bay Estuary (Figure 2.1). Tides are semi-diurnal with a maximum range of 1.8 m. By virtue of its location and orientation, Careel Bay is well-protected from ocean swell. The bay is shallow and during low tide it is nearly cut-off from Pittwater by an extensive sand bar. Seagrass beds (primarily Zostera capricorni Ascherson and Posidonia australis Hooker) occur between the opening of Careel Bay and Pittwater and abut the seaward edge of the mangrove swamp (indicated by dense peg roots and saplings of Avicennia marina (Forst.) Vierh., the grey mangrove). Henceforth this zone shall be referred to as the 'seaward zone.' The commercial oyster Saccostrea cucullata (Born) occurs in a few small clumps (less than 3-4 m^2) around the bases of the trunks and on some peg roots of A. marina at this interface between mangroves and seagrasses. The seaward two-thirds of the forest proper (i.e. where the mangroves grow as tall trees (5-6 m high) with a dense, almost continuous, canopy) consists entirely of the grey mangrove. A shorter (< 2 m) and more shrub-like second species, the river mangrove Aegiceras corniculatum (L.) Blanco, is sporadically interspersed with A. marina within the landward one-third of the forest.

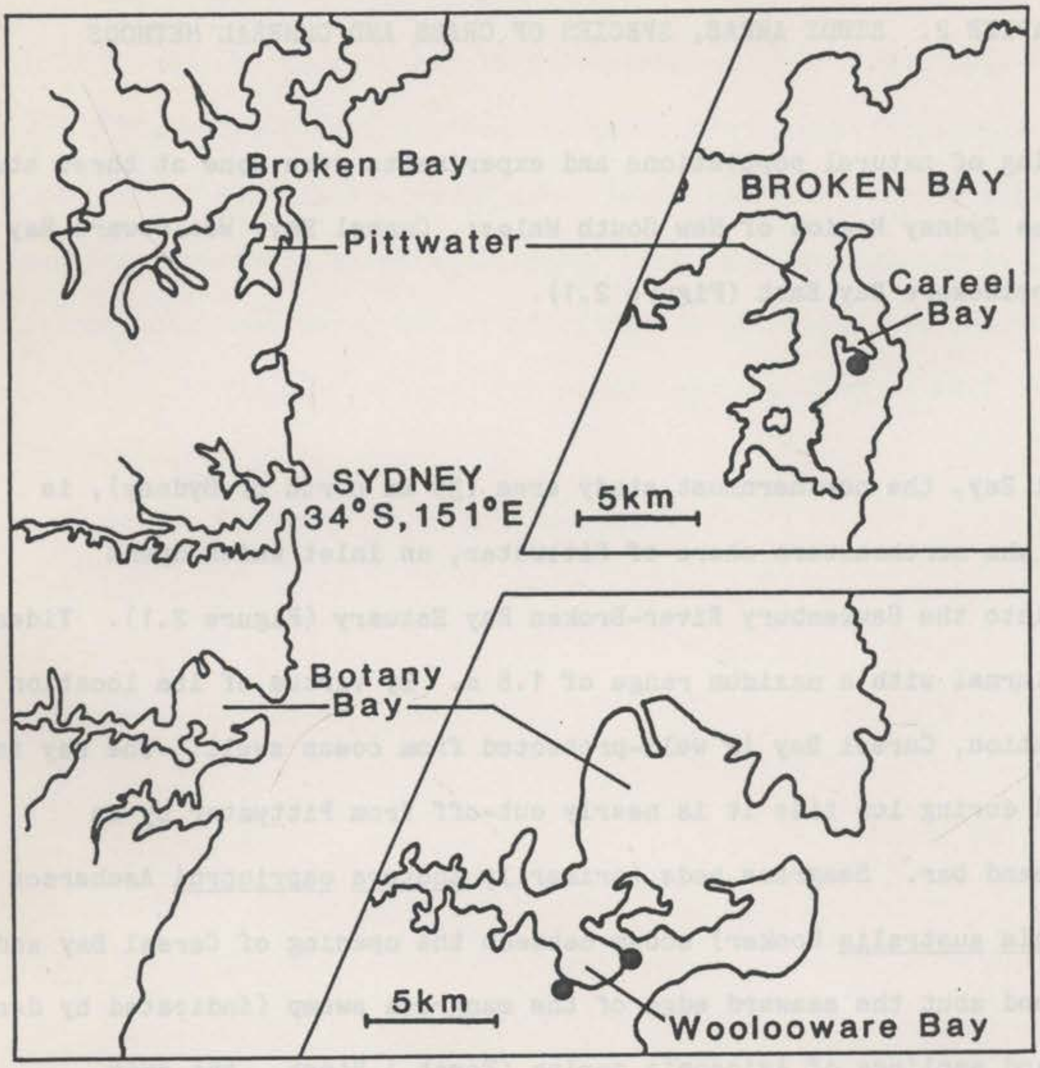

Figure 2.1. Maps of the Sydney region, with insets of the study areas (●) at Careel Bay and Woolooware Bay.

Where the forest proper occurs will hereafter be called the 'midmangrove zone.' A fairly sudden decline in the height and density of A. marina occurs at the landward edge of this zone. This marks the interface of the mangrove swamp with the salt marsh. This interface, referred to as the 'landward zone', is characterised by short, shrubby grey and river mangroves, peg roots of the grey mangrove and scattered clumps of the samphire Sarcocornia quinqueflora (Bunge ex Ungern-Sternberg) and various grasses (e.g. Sporobolus virginicus (L.) Kunth). Mangroves are dispersed throughout the salt marsh which has been severely truncated at the landward edge by residential and recreational development. Most salt marshes near Sydney grade into stands of the needlerush Juncus krausii (Hochst.) and she-oak Casuarina glauca (Sprieng.) Sieb. which frequently give rise landward to eucalypt forest. At Careel Bay, however, the saltmarsh and portions of the midmangrove and landward zones abut backyard lawns, clotheslines, etc.

Although the zones within the portion of the mangrove swamp in which I worked are irregularly shaped, their approximate areas are presented in Table 2.1.

The nature of the substratum varies markedly from the seagrass beds landward to the salt marsh. Because of the extensive sand bar described earlier, the sediments of the seagrass beds are composed of a greater proportion of sand (and less silt) than those of seagrass beds adjacent to most mangrove swamps near Sydney. These sediments are consolidated enough to support the weight of someone walking across them at low tide. An attempt at the same feat seaward of most other mangrove swamps would result in one sinking thigh-deep (or deeper) once beyond the zone of dense peg roots. The

Table 2.1. Approximate dimensions of the 3 mangrove zones at Careel Bay, Woolooware Bay West and Woolooware Bay East. The first dimension was measured parallel to the shore; the second dimension was measured in a seaward-landward direction.

	DIMENSIONS (m)		
ZONE	CAREEL BAY	WOOLOOWARE BAY WEST	WOOLOOWARE BAY EAST
Seaward	144 x 8	152 x 10	224 x 13
Midmangrove	194 x 128	157 x 93	235 x 72
Landward	136 x 7	220 x 8	257 x 8

sediments within the seaward zone of the mangroves appear (at least superficially) similar to those of the seagrass beds, but the dense peg and nutritive roots of A. marina create a more consolidated substratum. Numerous burrows of crabs, callianassid shrimps and other decapods and abundant molluscan shells create large air spaces within the top 30-40 cm of substratum.

The substratum in the midmangrove zone is infiltrated with a greater density of nutritive roots than in the seaward zone and is comprised primarily of sand with a lesser proportion of silt. Peg roots are of similar density to that of the seagrass beds, but the greater density of nutritive roots results in a very consolidated substratum which can be dug up and carried as a cube of material. The abundance of oysters and the shells of these and other molluscs, and the extent of the network of burrows (and other large air spaces), are also less in this zone and contribute to the greater solidity of the substratum.

Sediments in the landward zone have a still greater proportion of sand and less silt than in the midmangrove zone, but the smaller density of peg roots and nutritive roots results in a less consolidated substratum which falls apart easily when exhumed. Nonetheless, the ground provides a quite solid surface on which to walk. The substratum in the salt marsh is similar, but the peg roots and nutritive roots of A. marina are found only adjacent to the scattered individuals of this species.

Woolooware Bay

The two other study areas were located on the western and eastern shores of Woolooware Bay, 20 km south of Sydney (Figure 2.1). The distance across the shallow bay (between the two areas) is approximately 2 km. The entire perimeter and most of the interior of the bay is leased for the mariculture of oysters. Woolooware Bay is one of three large bays opening into the southern portion of Botany Bay. With its two tributaries, the Georges and Cooks Rivers, Botany Bay forms a vertically well-mixed estuary (Rochford 1951). Tides are as described for Careel Bay. Although Botany Bay is subject to ocean swell, the position and orientation of the entrance to Woolooware Bay protect it from strong waves (Rochford 1951).

Seaward of the study area at Woolooware Bay West are extensive, unconsolidated mud flats. The sediments of the seaward zone are consolidated somewhat by the great density of peg roots of A. marina, but the substratum is much siltier and looser than that of the seaward zone at Careel Bay. The network of burrows and air spaces is also less extensive here than at Careel Bay, probably because the substratum is more fluid in this zone at Woolooware Bay West. Live and dead oysters are abundant on the trunks of most trees and on some peg roots. The midmangrove zone is much like that at Careel Bay, in terms of consolidation of sediments and other physical attributes, but A. corniculatum is much less abundant, and the extent of the midmangrove zone here (along an axis running seaward and landward) is about 25% smaller than that at Careel Bay (Table 2.1). Virtually all of the salt marsh and some of the landward zone of mangroves have been filled in for industrial or recreational development. The only evidence of a vegetational affinity with other salt marshes is the presence of a few scattered individuals or patches of Sarcocornia and Juncus. A steep (1-1.5 m high) berm of terrestrial vegetation abuts the landward zone of peg roots or, in a few areas, the landward fringe of the trees (trunks) themselves. Other than these perturbations, the majority of the mangrove swamp at Woolooware Bay West appears relatively undisturbed (with respect to the health of the mangroves and the abundances of typical mangrove fauna).

Although the third study area is near the one just described, Woolooware Bay East varies in a number of characteristics from its western counterpart and is more similar in other respects to the more distant swamp at Careel Bay. The silty and unconsolidated substratum seaward of the peg roots on the eastern side of the bay supports extensive seagrass beds of Zostera and Posidonia. Much of this area is occupied by wooden piers used for the culture of oysters. Oysters are more abundant in the seaward and lower midmangrove zone here than at the other two sites. The degree of consolidation of the sediments and the extent of burrows and other large air spaces is intermediate between the two other swamps.

The seaward zone itself is broader (in a seaward-landward direction) than at the other two study areas (Table 2.1). The nature of the substratum and mangroves in the midmangrove zone is similar to that described for the other two areas, but A. corniculatum are much more abundant in the upper one-third of this zone and in the landward zone here than at Careel Bay or at Woolooware Bay West. The substratum in the landward zone is similar to those in the other two areas. The salt marsh is expansive and is interrupted only by a narrow, unsealed track running between the nearby main road and Towra Point (at the extreme eastern boundary of Woolooware Bay). The salt marsh is

Table 2.2. List of the species of crabs encountered in the three study areas.

Family Ocypodidae

Heloecius cordiformis (H. Milne Edwards)
Australoplax tridentata (A. Milne Edwards)

Family Grapsidae

Sesarma erythrodactyla Hess
Paragrapsus laevis (Dana)
Helograpsus haswellianus (Whitelegge)
Helice leachi Hess
Ilyograpsus paludicola (Rathbun)

Family Xanthidae

Pilumnopeus serratifrons (Kinahan)

owned by two sand-mining companies (which have not actually mined material from anywhere within sight of the study area), and the track is administered by the National Parks and Wildlife Service, two factors contributing to the very low level of disturbance at Woolooware Bay East. The salt marsh is carpeted with Sarcocornia which is sporadically interrupted by stands of Sporobolus, other grasses and Casuarina.

Several criteria were used in the final selection of these three areas from among 25 swamps visited between October and December 1982. Of the swamps visited, 8 were initially selected because they afforded greater ease of access on foot from the main road and appeared relatively undisturbed in the three zones in which mangroves occurred. The crabs in these swamps were censused in December 1982, and the abundances of the three focal species were generally greater at Careel Bay and at both areas at Woolooware Bay than at the other five swamps. These three areas also appeared to be largely ignored by the public and experiments would not be vulnerable to vandalism or other interference. Lastly, all areas were within one hour's drive from the University of Sydney.

Species of Crabs

Eight species of crabs were encountered in the mangrove zones of the three study areas (Table 2.2). Of these, Ilyograpsus paludicola, Pilumnopeus serratifrons, and Helice leachi were caught only occasionally in pitfall traps (the former two in the seaward zone and the third in the landward zone). Australoplax tridentata were abundant in the lower two zones of all three swamps and Helograpsus haswellianus were occasionally trapped in large numbers in the landward zone of Woolooware Bay West and in smaller numbers at the other two study areas. The remaining three species were abundant in all three swamps and served as the focal animals of this study. All three inhabit burrows and are active on the surface of the substratum only during periods of emersion. The sexes are dimorphic with adult males having much larger chelae than adult females.

The most conspicuous species of crab on the surface is an ocypodid, Heloecius cordiformis (Griffin 1971; Yates 1978; Figure 2.2A). Crabs of this species excavate burrows to a maximal depth of 40 cm (although most are < 25 cm deep). These burrows are blind-ending tubes with a single entrance, which has a characteristically round shape and is unambiguously identifiable as having been made by this species. H. cordiformis defend their burrows from intruders and remain fairly close to the burrow when engaged in most activities on the surface. Like their ocypodid relatives, the fiddler crabs, H. cordiformis feed by sifting through the top few millimetres of substratum, extracting particles of food on or within the sediments and ejecting pellets of sand mixed with mucus (Griffin 1971). Although the diet of this species has not been quantitatively examined, it is thought to consist of the same sorts of items consumed by fiddler crabs: detritus, algae and micro-organisms (Crane 1975; Fielder 1970; Miller 1961). They also have been observed picking and consuming algae from peg roots. H. cordiformis can attain a maximum carapace length (measured from the front of the carapace to the suture before the abdomen) of 25 mm, but crabs of this size are common only in the salt marshes landward of the mangrove forest. Crabs in the present study rarely exceeded 20 mm.

Figure 2.2. The three species of crabs investigated in this study and the carapace length of each specimen. All photographs are of males. (Photographer: Kathie Atkinson)

A. Heloecius cordiformis (24 mm)

B. Paragrapsus laevis (33 mm)

C. Sesarma erythrodactyla (28 mm)

The largest of the three species is Paragrapsus laevis, the purple shore crab (Figure 2.2B). It is an omnivore which may attain a maximum carapace length of approximately 40 mm. It is a more secretive species than H. cordiformis: when the crabs emerge from their burrows, they either remain motionless at the entrance or scuttle along submerged channels under debris that accumulates there. Dissection of the cardiac stomachs of 7 individuals revealed fragments of algae, clam shells and of the two other species of crabs examined in this study. On several occasions, P. laevis were observed to attack other crabs and either consume them on the surface or drag their prey into their burrows. One of these events involved a large male attacking a smaller conspecific. These crabs might also be scavengers. The burrows of P. laevis are generally deeper than those of H. cordiformis (frequently 30-40 cm) and the entrance is ovate or irregular rather than circular. This species has never been observed excavating or otherwise maintaining or repairing burrows, and the crabs frequently do not return to the same burrows after an excursion (unlike H. cordiformis).

The third species studied was another large grapsid, Sesarma erythrodactyla, the red-fingered shore crab (Figure 2.2C). The maximum carapace length is approximately 30 mm, but individuals of this size are much less common than P. laevis of similar size. It is a skittish species which inhabits deep burrows with an oval or irregularly-shaped entrance and has not been observed excavating nor repairing these burrows. Also like P. laevis, when S. erythrodactyla makes an excursion from the burrow, the crabs move far from the burrows (usually metres away) and rarely return to the one from which they emerged. This species has the unusual habit of climbing trees, and the sharply pointed dactyls on the ambulatory legs assist it in doing so.

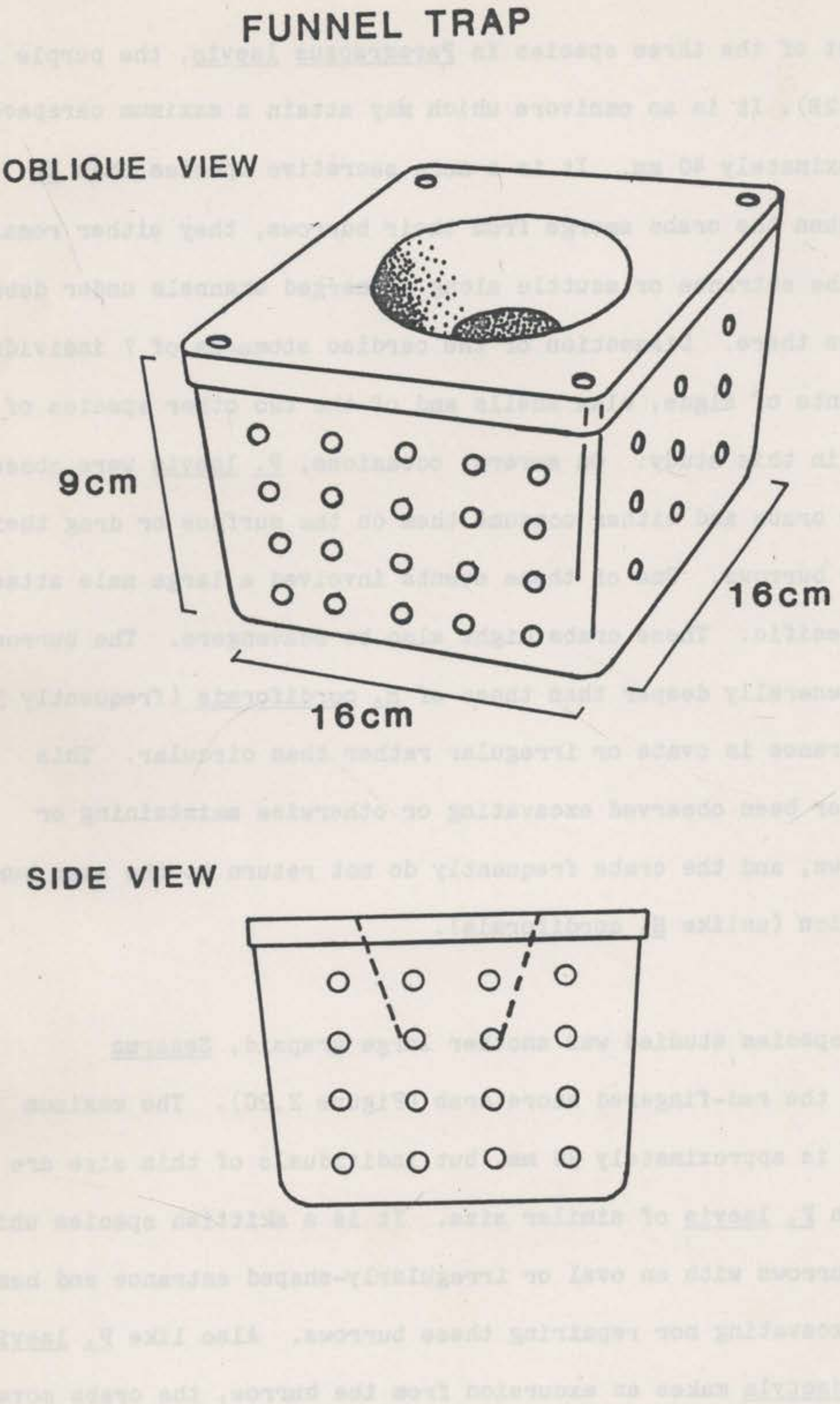

Figure 2.3. Pitfall trap for sampling crabs (after Yates 1978).

They are omnivorous scavengers and have been observed picking at algae growing on peg roots, macroalgae deposited by the tide and mangrove leaves lying on the substratum. Frequently, these leaves are dragged into the burrow, and burrows with a rolled leaf protruding from the entrance are a common sight. Occasionally, an individual has been observed carrying about or picking at carrion (usually a dead crab). Examination of 10 cardiac stomachs confirmed the diet described here from field observations.

General Methods

Methods that were used repeatedly for various aspects of this research are described here. Modifications of these methods and special methods designed for a particular experiment are described within the chapters to which they pertain.

1. Censuses to determine distributions and abundances

Two very different methods were used to census the three species in this study: baited pitfall traps and direct visual counts. A pitfall trap consisted of a perforated, plastic box (2-litre volume) and lid. A funnel was glued to the inner surface of the lid, under a circular hole cut from its centre (based on a design by Yates 1978; Figure 2.3). The baits were 40-50 g pieces of sardine wrapped in nylon mesh to prevent consumption by crabs. Baits were wired into the base of the trap to prevent them from floating and providing a raft which might have allowed access to the funnel and subsequent escape by crabs. Traps were buried flush with the surface of the substratum. Because the substratum in the seaward zone was relatively unconsolidated, the perforations in the base of the traps could become clogged and result in traps floating out of the substratum. To prevent this, traps in the seaward zone were weighted with approximately 50 g of lead. Lead is a fairly inert substance and was assumed to have a negligible effect on the number and species of crabs collected. Pitfall traps readily trapped P. laevis, S. erythrodactyla and all the other crabs listed in Table 2.2, except for H. cordiformis. This species only rarely fell into traps although it was always the most abundant species on the surface of the substratum (Yates 1978; Chapter 3, this study).

The small numbers of H. cordiformis found in baited traps were not surprising given its non-carnivorous habit. A pilot experiment which omitted baits from half of the pitfall traps indicated that omitting baits did not increase the number of H. cordiformis caught. Because data from pitfall traps were not, therefore, an appropriate estimate of the distribution or abundance of this species, crabs were censused by direct visual counts. To sample natural (i.e. non-experimental) populations, the numbers of crabs emerging from burrows within a 0.25 m^2 quadrat were counted within a 10-minute period after appearance of the first crab. If no crab emerged within a 10-minute waiting period, the quadrat was scored a zero, since H. cordiformis usually emerge within 5 minutes of placement of quadrats. This method was also used to census crabs in experimental enclosures, except that an experimental barrier (and not a quadrat) delimited the area being censused. Although P. laevis and S. erythrodactyla could also be censused in this way, they did not emerge from their burrows as readily as H. cordiformis (taking much longer to emerge, if they emerged at all).

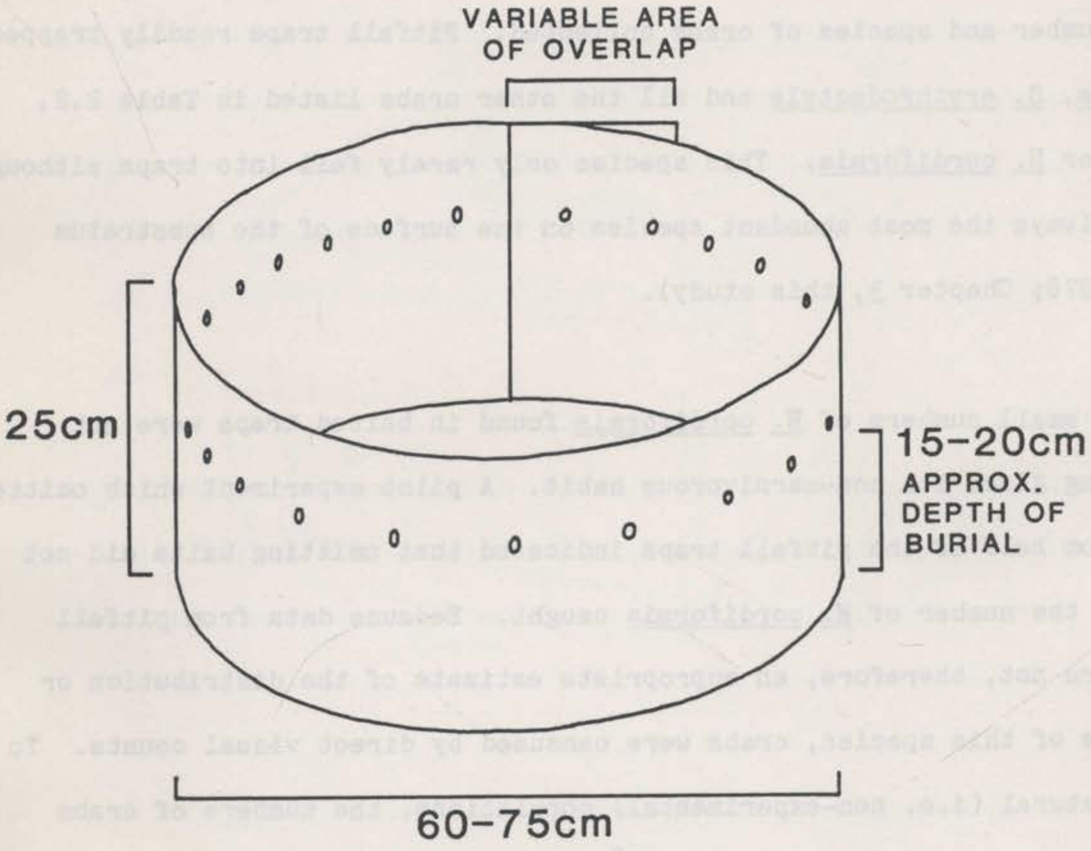

Figure 2.4. Formica barrier used to enclose crabs. The shape of enclosures was elliptical or circular. The minimal and maximal axes of elliptical enclosures were 60 cm and 75 cm, respectively.

2. Enclosures

Formica barriers were used for two principal applications: sampling microhabitats by pitfall traps and experiments requiring repeated censuses of a given group of crabs. Because crabs may easily traverse the interface between microhabitats, an unenclosed pitfall trap in one microhabitat might collect crabs occupying burrows in another microhabitat. To prevent this during the sampling of a particular microhabitat, barriers were placed around the trap and enclosed only a single type of microhabitat. Barriers were made from strips of formica (2.5 m x 0.30 m) bent into a circle or oval enclosing approximately 0.35-0.45 m^2 (Figure 2.4). These were buried to a depth of 15-20 cm to prevent crabs from burrowing into or out of the enclosed plot. Solid barriers were used because of the great difficulty in burying mesh fences below the surface of mud full of nutritive and peg roots. Several holes (5 mm in diameter) were drilled through the barriers to allow rapid drainage of water as the tide fell. Each barrier was covered with nylon flyscreen (1 mm mesh) to prevent crabs from entering or leaving the enclosure.

Nearly all field experiments (e.g. testing habitat preferences, interspecific interactions, effects of crabs on the substratum, etc.) required barriers to enclose experimental animals. These enclosures were identical to those described above for the sampling of microhabitats.

3. Collecting and marking crabs

Crabs used in experiments were collected by hand and by unenclosed, baited pitfall traps. Approximately 150 <u>H. cordiformis</u> per hour could be collected by hand. This was accomplished by trapping crabs in the upper few centimetres of the burrow by a finger or chopstick pushed through the substratum at an angle to the tunnel below the unsuspecting crab. By subsequently pushing the tip of the finger or chopstick upwards under the crab, the animal could be pushed from the burrow and collected. Because of the more elusive behaviour and deeper burrows of P. laevis and S. erythrodactyla, less than 50 crabs of these species could be collected per hour by this method; therefore, catches from pitfall traps were used to supplement those taken by hand. Daily catches of crabs were brought back to the laboratory and maintained in seawater tables until enough crabs had been collected to start the experiment (usually less than 5 days).

In several experiments, crabs had to be marked or individually numbered. Such crabs were brought to the laboratory and kept in perforated, rectangular bins (30 cm x 45 cm x 16 cm deep) lined with paper towels. To reduce the number of crabs injured or killed in fights, rocks were placed in the boxes to provide refuges. Approximately one-third of the bottom of each bin was immersed in 10-15 mm of seawater in a recycling system at the Ross Street Marine Laboratory (University of Sydney). Crabs maintained in this way survived well during the 5-7 days needed to mark all experimental animals.

Crabs to be marked or numbered were first rinsed with seawater to remove sand and mud and then were dried by placing them in plastic bins lined with dry paper towels and placed in a fume hood (with the fan running) for 30-60 minutes. White latex paint, applied with a fine brush, or fine-tipped white paint pens were used to put numbers or other marks on the dorsal surface of the carapace. To prolong the duration and legibility of marks, these were coated with quick-drying, transparent epoxy cement. When the cement had dried, crabs were returned to bins that were submersed as before. Subsequent behaviour of marked crabs suggested than relatively few crabs were injured or otherwise affected by this procedure. At the start of the field experiments, the few crabs which appeared 'sluggish' were not used and were released away from experimental enclosures.

Statistical Analyses

The majority of the aims of this research involved testing hypotheses formulated from preliminary observations of natural history. Designs for sampling natural and experimental populations included appropriate controls and replicates. Most of the hypotheses were tested by analyses of variance (the assumptions and methods of which are described in Snedecor and Cochran 1980, Winer 1971, and Underwood 1981). The assumption of homogeneity of variances was always evaluated by Cochran's test and, when necessary, data were transformed to reduce heteroscedasticity. When heterogeneity of variances was unresolvable by standard transforms, this is indicated in the text and tables associated with the given analysis of variance. When results of analyses of variance were significant, Student-Newman-Keuls (SNK) tests were used to determine which means differed from others. In tables, results from SNK tests are represented by the symbols >, < and =, indicating means that were significantly greater, smaller or not significantly different from other means. In these and all other statistical tests, a probability of 0.05 was considered a significant departure from results predicted by the null hypothesis.

CHAPTER 3. IDENTIFICATION OF DISTRIBUTIONAL PATTERNS

Introduction

The first aim of this study was to identify the distributional patterns of three common species of burrowing crabs among three tidal zones in three local mangrove swamps (described in Chapter 2). Preliminary observations suggested that within each zone, these species were not distributed evenly: Heloecious cordiformis appeared to be more abundant in well-drained mounds whereas Paragrapsus laevis was most abundant in moist or submerged flat areas, and Sesarma erythrodactyla seemed to occupy both of these 'microhabitats' with similar frequency. An ancillary aim of the sampling programme, therefore, was to determine if this pattern within zones was statistically significant.

Because distributions of organisms are usually patchy in time and space, sampling was designed to examine this variability at several scales. The larger of two spatial scales considered was variability among swamps. Although a species might have a statistically significant zonal pattern in all swamps, the nature of that pattern might differ from shore to shore (e.g. greatest density low on the shore in one swamp yet high on the shore in another). The same might apply to distribution between mounds and flats. These differences might be the result of variability in the extent of zones or microhabitats, differences in characteristics of the substratum (e.g. nutrients, oxygen, pH, distribution of grain-size, etc.), degree of human interference, or variability from other factors operating on a scale of at least kilometres. For this reason, three swamps were censused.

The smaller spatial scale allowed measurement of variability in abundances of crabs within a given zone (or microhabitat) but between sites separated by 15-25 metres, parallel to the shore. This design would be able to detect whether animals were distributed randomly in the three tidal zones examined. Replication within, in addition to among, zones was also necessary to validate whether suspected zonal patterns were related to differences in height on the shore or whether they were simply the result of sampling in any two distinct areas within a swamp.

Two temporal scales were also incorporated into the sampling programme. The larger one consisted of censusing swamps quarterly throughout the first year of this study (December 1982 - January 1984). Season was thought to be an important source of variability because at least one species (*H. cordiformis*) is only rarely observed on the surface during winter, and the apparent abundance of *S. erythrodactyla* was shown to differ significantly among monthly censuses in a nearby swamp (Yates 1978). If these changes are not similar among tidal zones or microhabitats, seasonal factors might then affect the nature of distributional patterns observed at other times of the year. Several studies have already shown that some species of crabs have reproductive migrations wherein the females move from higher levels in the swamp to the seaward edge to release their eggs (Ono 1959; Warner 1967). In the present study, data from traps and quadrats were used to determine if distributional patterns among zones and between microhabitats were spatially and temporally stable (or at least predictable). Although replication of sampling among seasons was done only for summer (for zonal censuses), and therefore long-term seasonal effects could not be rigorously tested, the

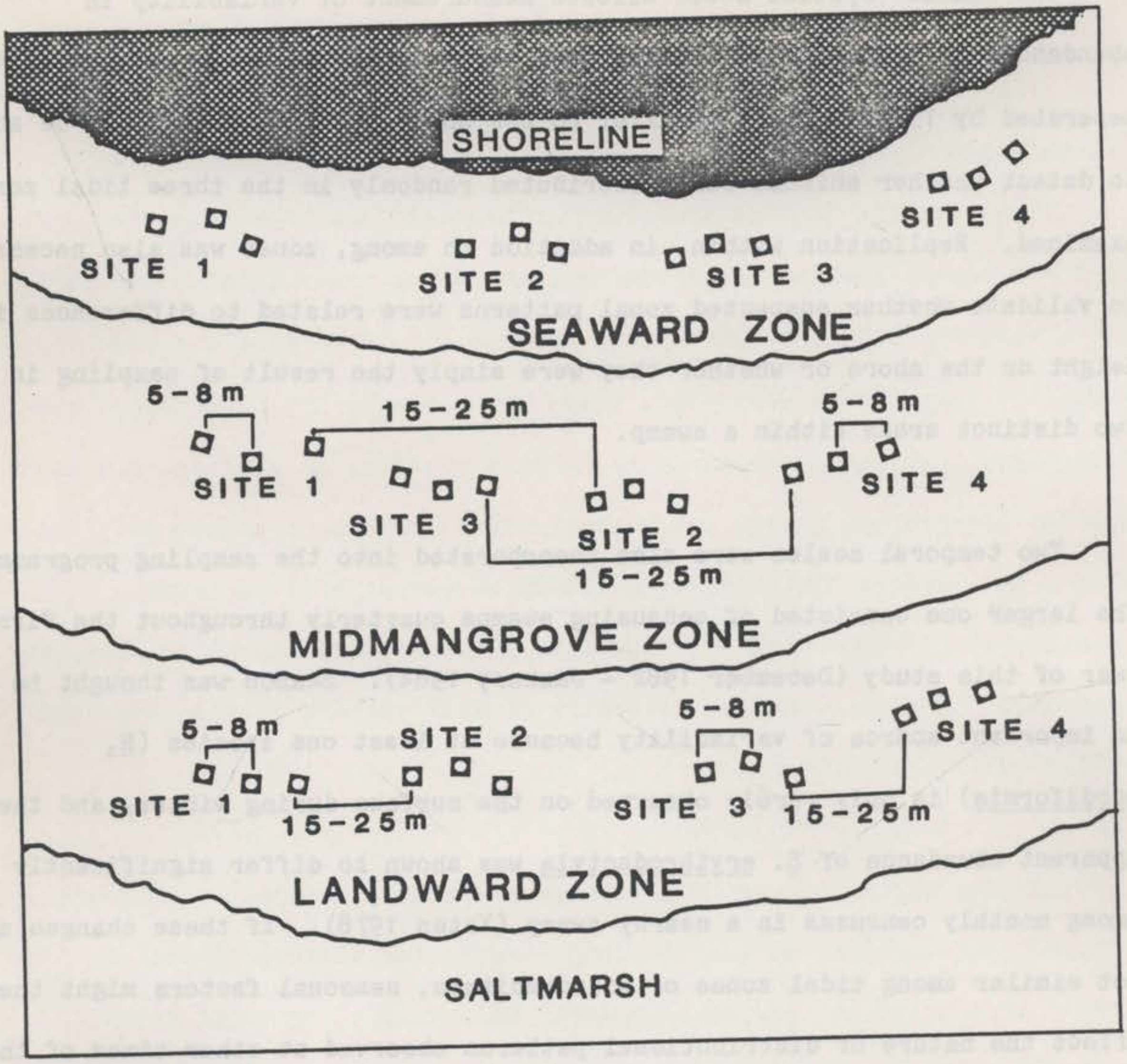

Figure 3.1. Spatial arrangement of traps and quadrats used to sample zones. Traps at Sites 1 and 2 were put out on Day 1, censused and re-buried at Sites 3 and 4 on Day 3, and censused and removed on Day 5. Quadrats at Sites 1 and 2 were censused on Day 1; quadrats at Sites 3 and 4 were censused on Day 3. ☐ = trap or quadrat.

results from this study provide a preliminary view of seasonal patterns which may be occurring from year to year.

The smaller temporal scale allowed examination of the potential variability between two sampling efforts within a week. Day-to-day differences in apparent abundances of crabs could result from differences in tidal phase, time of day, or atmospheric conditions which might then affect endogenously controlled levels of activity. Sampling on this small scale was also necessary to determine if the magnitude of difference in distribution and abundance among seasons was greater than that expected from day to day. Without this analysis, differences from one quarterly census to the next might actually reflect differences between any two censuses and not necessarily indicate seasonal effects.

Methods and Materials

1. Sampling of zones

Quadrats were used to sample H. cordiformis and S. erythrodactyla (see Chapter 2 for details of this method). P. laevis only occasionally appeared in censuses with quadrats; these few data were, therefore, not used in statistical analyses. On the first day of sampling, two groups of 3 quadrats were censused within each tidal zone. Each group of quadrats constituted a 'site' and was 15 to 25 m away from the other group. Quadrats within a group were 5-8 m apart (Figure 3.1). All six quadrats sampled areas of substratum at approximately the same distance from the seaward edge of the swamp (i.e. similar tidal height within a zone). The procedure was repeated 2 days later. Within this design, sites from Day 1 and Day 3 could, at least theoretically overlap; however, the study areas were large relative to sites and overlap occurred only rarely (at most twice). Sampling for each season, therefore, consisted of censuses done on two days in each swamp.

Baited pitfall traps were used to sample the distributions of P. laevis and also S. erythrodactyla (see Chapter 2 for description of traps and baits). On the first day of sampling, two groups of three traps were buried in each tidal zone. Burial of traps in a line parallel to the shore ensured similar duration of emersion and submergence. Two days later, traps were opened and crabs were identified, counted, measured (carapace length) and released at the pit formerly containing the trap. Fresh baits were then wired into traps which were buried in new sites, in the spatial arrangement already described for quadrats. The second set of traps was opened after two days and crabs were censused and released as above.

A pilot sampling study, using 3 traps (censused once) in one site per zone, was done at all three swamps in December 1982, but quadrats were not used. In May 1983, a design of intermediate complexity involved censusing four traps and quadrats per zone on one day, in one site, and sampling in a different site two days later. Subsequent censuses on the larger scale described above were done with traps and quadrats in July and October 1983, and in January 1984.

In December 1982, only the variations among mangrove swamps, species and zones were examined, because only one sampling effort (Day) and one site per zone were involved. Initial analyses of data from subsequent censuses indicated no consistent effect of either Day or Site on the mean number of crabs per trap or quadrat; therefore, consistent significant differences between zones and between quarterly censuses would not result merely from differences between consecutive sampling efforts. To simplify subsequent analyses, day and site were combined into a single factor, Sampling Unit. A Sampling Unit, then, consisted of a group of 3 traps (or quadrats) and each census of a swamp included 4 Sampling Units per zone. Sampling Units were nested within Zones; the other three factors (Mangrove swamps, Species and Zones) were orthogonal.

In many cases, data had to be transformed to resolve heterogeneous variances. Transforms of 1) $\sqrt{x+1}$, 2) ln (x+1) or 3) $x^{0.25}$ led to non-significant Cochran's tests in all analyses.

2. Sampling of microhabitats

Traps (enclosed within formica barriers) and quadrats were also used to determine the distribution of crabs in mounds and flats (see Chapter 2 for details of barriers). The placement and sampling of traps and quadrats followed the same spatial and temporal arrangement as described for sampling zonal distributions, except that 2 sets of 3 traps (or quadrats) constituted a 'site' (i.e. 3 traps, or quadrats, in flats and 3 in mounds). Censusing of microhabitats, because of the much greater requirement of time and materials, was done only at Careel Bay during the first year of sampling and at both study areas at Woolooware Bay during the second year of sampling. The first census at Careel Bay (May 1983) was done in the two upper zones. So few crabs were caught in traps in the landward zone (because all three species are least abundant in this zone) that analyses of differential occupation of

Table 3.1. Summary of analyses of variance of the mean number of crabs per quadrat or trap used in the censuses of zones. ns = $P > 0.05$; * = $P < 0.05$; ** = $P < 0.025$; *** = $P < 0.01$; **** = $P < 0.001$. SU = Sampling Unit (see text for definition). ANOVA tables for these results are in Appendix 3.1. Sampling by quadrats was not done in December 1982. Few crabs emerged onto the surface during observations in July 1983; therefore, no analyses were done for quadrats.

A. DATA FROM QUADRATS (*H. cordiformis* and *S. erythrodactyla*)

SOURCE	DEC 82	MAY 83	JULY 83	OCT 83	JAN 84
Mangrove		ns		ns	*
Species		****		****	****
Zone		**		****	****
MAxSP		ns		ns	***
MAxZ		***		ns	**
SPxZ		*		****	****
MAxSPxZ		***		ns	ns
SU(MAxZ)		***		***	ns
SPxSU(MAxZ)		ns		ns	ns

B. DATA FROM TRAPS (*P. laevis* and *S. erythrodactyla*)

SOURCE	DEC 82	MAY 83	JULY 83	OCT 83	JAN 84
Mangrove	ns	*	****	**	ns
Species	ns	****	****	****	ns
Zone	ns	**	****	***	****
MAxSP	ns	****	****	****	ns
MAxZ	ns	ns	ns	ns	ns
SPxZ	ns	****	****	ns	**
MAxSPxZ	ns	**	ns	**	***
SU(MAxZ)	---	ns	****	***	**
SPxSU(MAxZ)	---	ns	****	***	***

microhabitats were inconclusive. Subsequent censuses at all three swamps were done in the midmangrove zone only.

At Careel Bay, crabs were sampled in the two microhabitats in May, July and October 1983, and in January 1984. At Woolooware Bay (West and East swamps), crabs were sampled in October 1985 and March 1986. Analyses and transforms were similar to those used for analyses of zonal patterns.

Results

Most of the analyses of distributional patterns indicated significant interactions between Species and Zones and between Species and Microhabitats ($\underline{P} < 0.05$; Tables 3.1-3.3, and Appendices 3.1-3.3); therefore, the patterns for each species will be discussed separately. Because of species-specific differences in the effectiveness of traps versus quadrats as sampling methods (see Chapter 2), results for H. cordiformis are from quadrats only, those for P. laevis are from traps only; and those for S. erythrodactyla are from traps and quadrats.

1. H. cordiformis

No single pattern best described the zonal distribution observed for H. cordiformis in all mangrove swamps in all seasons (Figure 3.2; Table 3.4). At Careel Bay, this species was always more abundant in the midmangrove zone than in the zones above and below. Three different patterns were indicated by SNK tests on data from the three censuses at Woolooware Bay East. In general, there was a tendency towards greater numbers being present in the midmangrove, or midmangrove and landward zones. At Woolooware Bay West, three patterns emerged: 1) decreasing abundance from the seaward to the

Table 3.2. Summary of analyses of variance of the numbers of crabs in mounds and flats at Careel Bay. In May 1983, the factor Zone was also tested (C, below). Few crabs were seen on the surface of the substratum in July 1983; therefore, no analyses of data from quadrats were done. Symbols and abbreviations as in Table 3.1. ANOVA tables for these results are in Appendix 3.2.

A. DATA FROM QUADRATS (*H. cordiformis* and *S. erythrodactyla*)

SOURCE	MAY 83	JULY 83	OCT 83	JAN 84
Species	****		***	****
Microhabitat	****		ns	****
SPxMH	****		***	****
SU(MH)	ns		*	***
SPxSU(MH)	ns		**	ns

B. DATA FROM TRAPS (*P. laevis* and *S. erythrodactyla*)

SOURCE	MAY 83	JULY 83	OCT 83	JAN 84
Species	ns	ns	ns	ns
Microhabitat	*	ns	ns	*
SPxMH	****	**	ns	***
SU(MH)	ns	ns	ns	ns
SPxSU(MH)	ns	ns	****	ns

C. DATA FROM MAY 1983 (when microhabitats in the midmangrove and and landward zones were censused)

SOURCE	TRAPS	QUADRATS
Species	ns	****
Zone	**	****
Microhabitat	*	****
SPxZ	*	ns
SPxMH	****	****
ZxMH	ns	ns
SPxZxMH	****	ns
SU(MHxZ)	ns	ns
SPxSU(MHxZ)	ns	ns

Table 3.3. Summary of analyses of variance of the numbers of crabs in mounds and flats during the second year of sampling at Woolooware Bay West and Woolooware Bay East. Symbols and abbreviations as in Table 3.1. ANOVA tables for these results are in Appendix 3.3.

A. DATA FROM QUADRATS (*H. cordiformis* and *S. erythrodactyla*)

SOURCE	OCTOBER 1985	MARCH 1986
Mangrove	***	ns
Species	****	****
Microhabitat	****	****
MAxSP	ns	***
MAxMH	ns	ns
SPxMH	***	****
MAxSPxMH	**	ns
SU(MAxMH)	ns	*
SPxSU(MAxMH)	ns	ns

B. DATA FROM TRAPS (*P. laevis* and *S. erythrodactyla*)

SOURCE	OCTOBER 1985	MARCH 1986
Mangrove	*	ns
Species	ns	**
Microhabitat	ns	**
MAxSP	ns	ns
MAxMH	ns	ns
SPxMH	**	****
MAxSPxMH	ns	ns
SU(MAxMH)	ns	ns
SPxSU(MAxMH)	*	ns

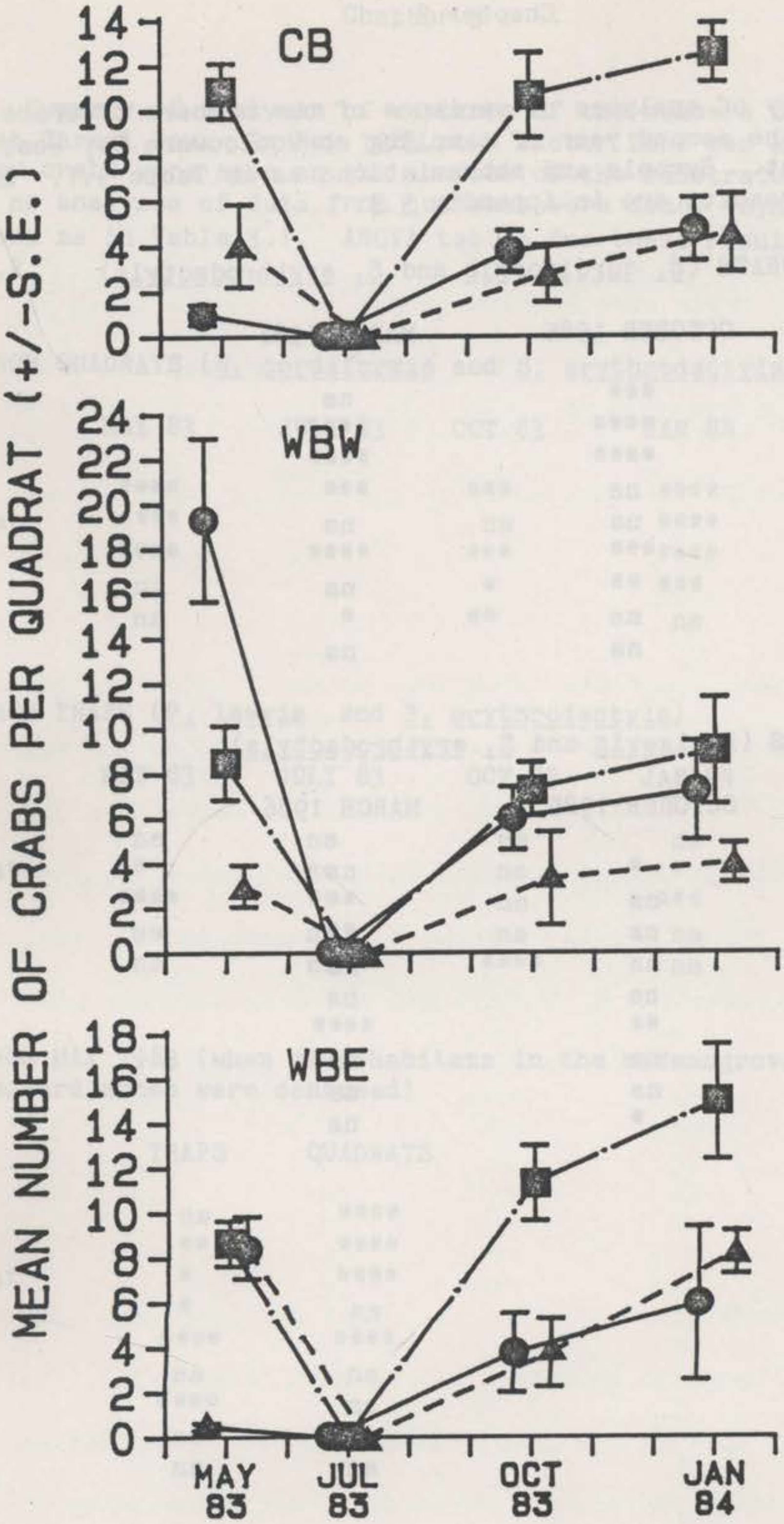

Figure 3.2. Mean number (+/- S.E.) of H. cordiformis per quadrat, for 3 mangrove swamps and 3 zones. CB = Careel Bay, WBW = Woolooware Bay West and WBE = Woolooware Bay East. Circles = seaward zone, squares = midmangrove zone, and triangles = landward zone.

Table 3.4. Mean number (+ S.E., untransformed) of *H. cordiformis* per quadrat for 3 mangrove swamps, 3 censuses and 3 zones. Sampling by quadrats was not done in December 1982. Few crabs were seen in July 1983; therefore, no analyses were done for this census. *n* = number of quadrats; Sampling Units have been pooled.

	TIDAL ZONE				
MANGROVE & CENSUS (*n*)	SEAWARD ZONE(A)	MIDMANGROVE ZONE(B)	LANDWARD ZONE(C)	SNK TESTS	*P*-VALUE FROM SNK TESTS
Careel Bay:					
May 83 (8)	1.00 (0.46)	10.80 (1.22)	4.00 (1.82)	B>A=C	< 0.001
Oct 83 (12)	3.75 (0.91)	10.58 (1.90)	2.75 (1.26)	B>A=C	< 0.001
Jan 84 (12)	4.67 (1.39)	12.42 (1.32)	4.50 (1.71)	B>A=C	< 0.001
Woolooware Bay West:					
May 83 (8)	19.30 (3.67)	8.50 (1.66)	3.00 (0.94)	A>B>C	< 0.001
Oct 83 (12)	6.00 (1.43)	7.33 (1.21)	3.33 (2.09)	A=B=C	> 0.05
Jan 84 (12)	7.25 (2.22)	9.00 (2.39)	4.00 (0.88)	A=B>C	< 0.05
Woolooware Bay East:					
May 83 (8)	0.50 (0.16)	8.60 (1.03)	8.40 (1.40)	B=C>A	< 0.001
Oct 83 (12)	3.75 (1.77)	11.25 (1.68)	3.75 (1.51)	B>C=A	< 0.001
Jan 84 (12)	5.92 (3.40)	14.83 (2.59)	8.17 (0.96)	B>C>A	< 0.01

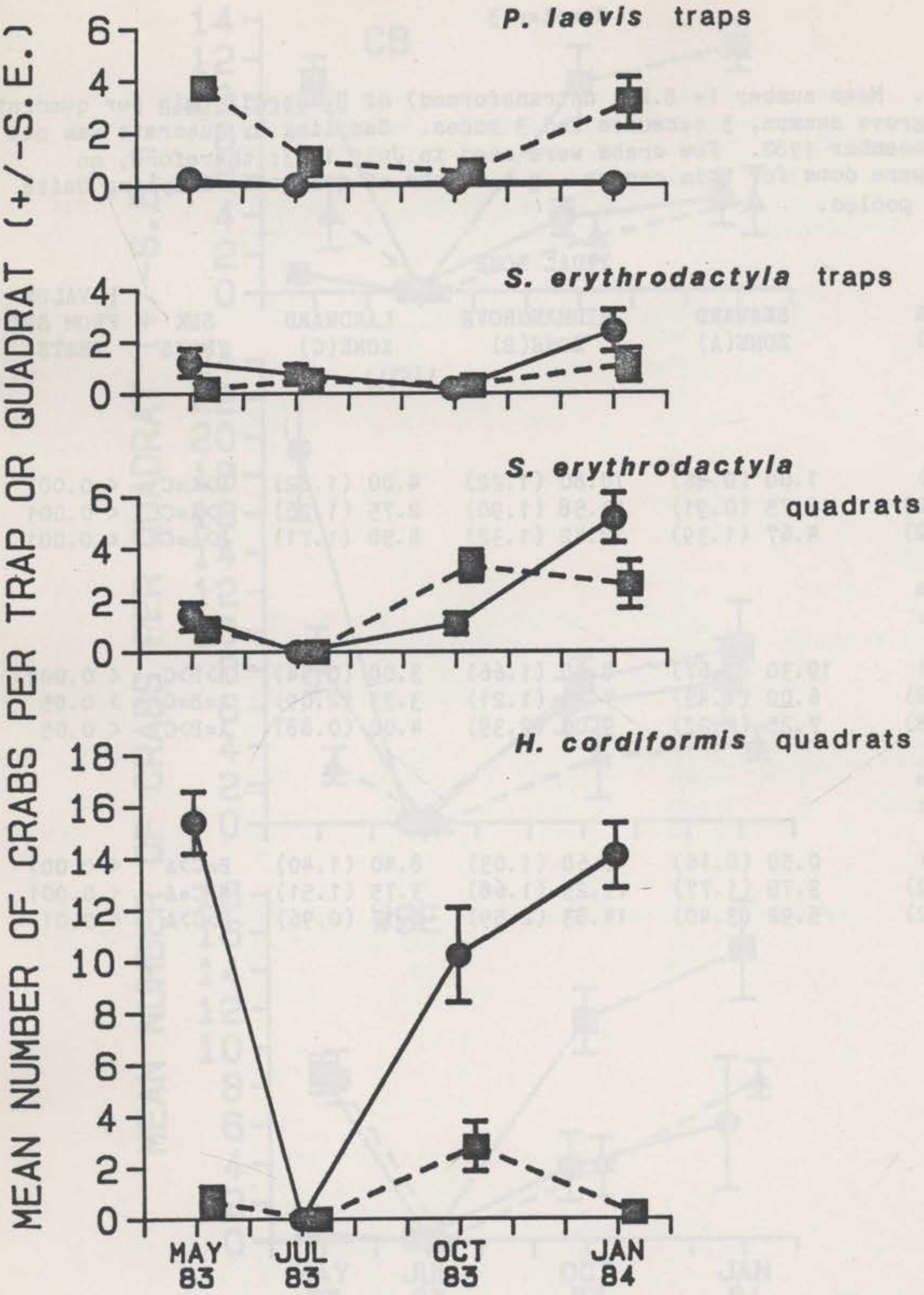

Figure 3.3. Mean number (+/- S.E.) of crabs per trap or quadrat in two microhabitats in the midmangrove zone at Careel Bay. Circles = mounds; squares = flats.

landward zone (May 1983), 2) similar abundances in all three zones (October 1983) or 3) similar abundance in the lower two zones with fewer crabs in the landward zone.

Virtually no H. cordiformis were observed on the surface during winter (July 1983). No other consistent effect of season on zonal patterns was indicated. The possible effect of season on the proportion of females in each zone (to assess the likelihood of seaward reproductive migration) could not be analysed from data collected from visual censuses of quadrats. The key feature typically used to discriminate males from females is the size (and sometimes colour) of the chelae: mature males have larger chelae than the females, and larger males have purple chelae; females never have purple chelae. In medium- to small-sized crabs, however, this sexual dimorphism is less obvious. Additionally, if the crab is facing away from the observer or peg roots obscure the claws, it is difficult to identify the sex of the crab. For all these reasons, counts of males, females and unknowns were thought to be too ambiguous for meaningful analysis of sex ratios.

For all censuses when H. cordiformis was active on the surface, these crabs were significantly more abundant in mounds than in flats (SNK tests, $P < 0.01$; Figure 3.3 and Tables 3.5-3.7). This pattern was consistent in all three swamps and in all seasons.

2. P. laevis

The distribution of P. laevis among zones reflected a fairly consistent pattern of significantly greater abundance in the lower two zones - the seaward and midmangrove zones (Table 3.8; Figure 3.4). The relationship

Table 3.5. Mean number (+ S.E., untransformed) of crabs per quadrat or per trap for 4 censuses of microhabitats in the midmangrove zone at Careel Bay. Neither Microhabitat nor Microhabitat x Species were significant in the analyses of data from traps in October 1983; therefore, no SNK tests were done. > and < indicate significant differences by SNK tests; = indicates no significant difference ($P > 0.05$). *n* = number of traps or quadrats. Sampling Units have been pooled.

SPECIES & CENSUS (*n*)	MICROHABITAT			*P*-VALUE FROM SNK TESTS
	MOUND		FLAT	
H. cordiformis: (quadrats)				
May 83 (8)	15.40 (1.21)	>	0.70 (0.62)	< 0.001
Oct 83 (12)	10.25 (1.85)	>	2.83 (0.96)	< 0.01
Jan 84 (12)	14.08 (1.27)	>	0.25 (0.25)	< 0.001
P. laevis: (traps)				
May 83 (8)	0.20 (0.12)	<	3.70 (1.09)	< 0.001
July 83 (12)	0	<	0.92 (0.53)	< 0.001
Oct 83 (12)	0.08 (0.08)	=	0.50 (0.17)	NONE
Jan 84 (12)	0.08 (0.08)	<	3.17 (0.97)	< 0.001
S. erythrodactyla (traps)				
May 83 (8)	1.20 (0.54)	>	0.20 (0.20)	< 0.01
July 83 (12)	0.75 (0.39)	=	0.50 (0.42)	> 0.05
Oct 83 (12)	0.17 (0.08)	=	0.33 (0.22)	NONE
Jan 84 (12)	2.42 (0.80)	>	1.08 (0.64)	< 0.05
S. erythrodactyla: (quadrats)				
May 83 (8)	1.40 (0.54)	=	0.90 (0.45)	> 0.05
Oct 83 (12)	1.08 (0.42)	=	3.33 (0.61)	> 0.05
Jan 84 (12)	5.17 (0.98)	=	2.58 (0.94)	> 0.05

Table 3.6. Mean number (+ S.E., untransformed) of crabs per quadrat or per trap for the census of microhabitats in May 1983. Data are from the midmangrove and landward zones at Careel Bay. *n* = 8 traps or quadrats. Sampling Units have been pooled. >, < and = as in Table 3.5.

	MICROHABITAT			*P*-VALUE FROM SNK TESTS
SPECIES & ZONE	MOUND		FLAT	
H. cordiformis: (quadrats)				
Midmangrove Zone	15.40 (1.21)	>	0.70 (0.62)	< 0.001
Landward Zone	8.30 (0.15)	>	0	< 0.001
P. *laevis*: (traps)				
Midmangrove Zone	0.20 (0.12)	<	3.70 (1.09)	< 0.001
Landward Zone	0.30 (0.22)	=	0.60 (0.32)	> 0.05
S. erythrodactyla: (traps)				
Midmangrove Zone	1.20 (0.54)	>	0.20 (0.20)	< 0.01
Landward Zone	0.50 (0.24)	=	0.50 (0.32)	> 0.05
S. erythrodactyla: (quadrats)				
Midmangrove Zone	1.40 (0.54)	=	0.90 (0.45)	> 0.05
Landward Zone	0.20 (0.20)	=	0.30 (0.22)	> 0.05

Table 3.7. Mean number (+ S.E., untransformed) of crabs per quadrat or trap for 2 censuses of microhabitats in the midmangrove zone at Woolooware Bay West and Woolooware Bay East. *n* = 12 traps or quadrats; Sampling Units have been pooled. <, > and = as in Table 3.5.

SPECIES & CENSUS	WOOLOOWARE BAY WEST			WOOLOOWARE BAY EAST		
	MOUND		FLAT	MOUND		FLAT
H. cordiformis: (quadrats)						
October 1985	5.92 (1.35)	>	0	9.92 (2.51)	>	0.08 (0.08)
March 1986	8.42 (1.43)	>	0	9.75 (0.91)	>	0
P. laevis: (traps)						
October 1985	0.67 (0.33)	<	1.75 (0.54)	0.08 (0.08)	<	0.67 (0.42)
March 1986	0.33 (0.25)	<	1.33 (0.42)	0	<	1.17 (0.61)
S. erythrodactyla: (traps)						
October 1985	0.75 (0.56)	<	0.17 (0.17)	0.50 (0.33)	=	0.67 (0.31)
March 1986	0.33 (0.23)	=	0.08 (0.08)	0.58 (0.25)	=	0.33 (0.25)
S. erythrodactyla: (quadrats)						
October 1985	0.75 (0.48)	>	0.33 (0.25)	1.00 (0.45)	<	1.42 (0.89)
March 1986	2.17 (0.67)	>	1.33 (0.60)	0.83 (0.39)	=	1.08 (0.73)

Table 3.8. Mean number (+ S.E., untransformed) of *P. laevis* per trap for 3 mangrove swamps, 5 censuses and 3 zones. Zone was not significant as a main effect nor in interactions in December 1982; therefore, no SNK tests were done. *n* = number of traps; Sampling Units have been pooled.

		TIDAL ZONE			
MANGROVE & CENSUS (*n*)	SEAWARD ZONE(A)	MIDMANGROVE ZONE(B)	LANDWARD ZONE(C)	SNK TESTS	*P*-VALUE FROM SNK TESTS
Careel Bay:					
Dec 82 (3)	0	1.00 (0.00)	0.67 (0.67)	NONE	
May 83 (8)	0.63 (0.24)	0.75 (0.60)	0.13 (0.13)	A=B=C	> 0.05
July 83 (12)	4.58 (1.09)	4.08 (1.23)	0	A>B>C	< 0.01
Oct 83 (12)	3.42 (1.75)	1.25 (0.82)	0	A>B=C	< 0.01
Jan 84 (12)	2.58 (1.21)	6.75 (2.10)	0.33 (0.33)	A=B>C	< 0.001
Woolooware Bay West:					
Dec 82 (3)	0.33 (0.33)	2.67 (2.19)	0.67 (0.33)	NONE	
May 83 (8)	2.50 (0.96)	0.63 (0.52)	0.38 (0.24)	A>B=C	< 0.05
July 83 (12)	15.75 (3.24)	17.38 (2.60)	1.92 (0.70)	A=B>C	< 0.001
Oct 83 (12)	7.42 (2.61)	8.88 (2.37)	3.67 (1.49)	A=B>C	< 0.05
Jan 84 (12)	2.58 (1.53)	3.50 (1.41)	0.92 (0.61)	A=B>C	< 0.05
Woolooware Bay East:					
Dec 82 (3)	0.33 (0.33)	1.33 (0.88)	0.33 (0.33)	NONE	
May 83 (8)	5.13 (2.13)	4.13 (1.71)	0	A=B>C	< 0.001
July 83 (12)	3.25 (1.43)	2.75 (1.05)	0	A=B>C	< 0.001
Oct 83 (12)	2.17 (0.98)	4.17 (1.09)	2.67 (1.57)	A=B=C	> 0.05
Jan 84 (12)	1.46 (0.41)	5.83 (1.27)	1.38 (0.47)	B>A=C	< 0.01

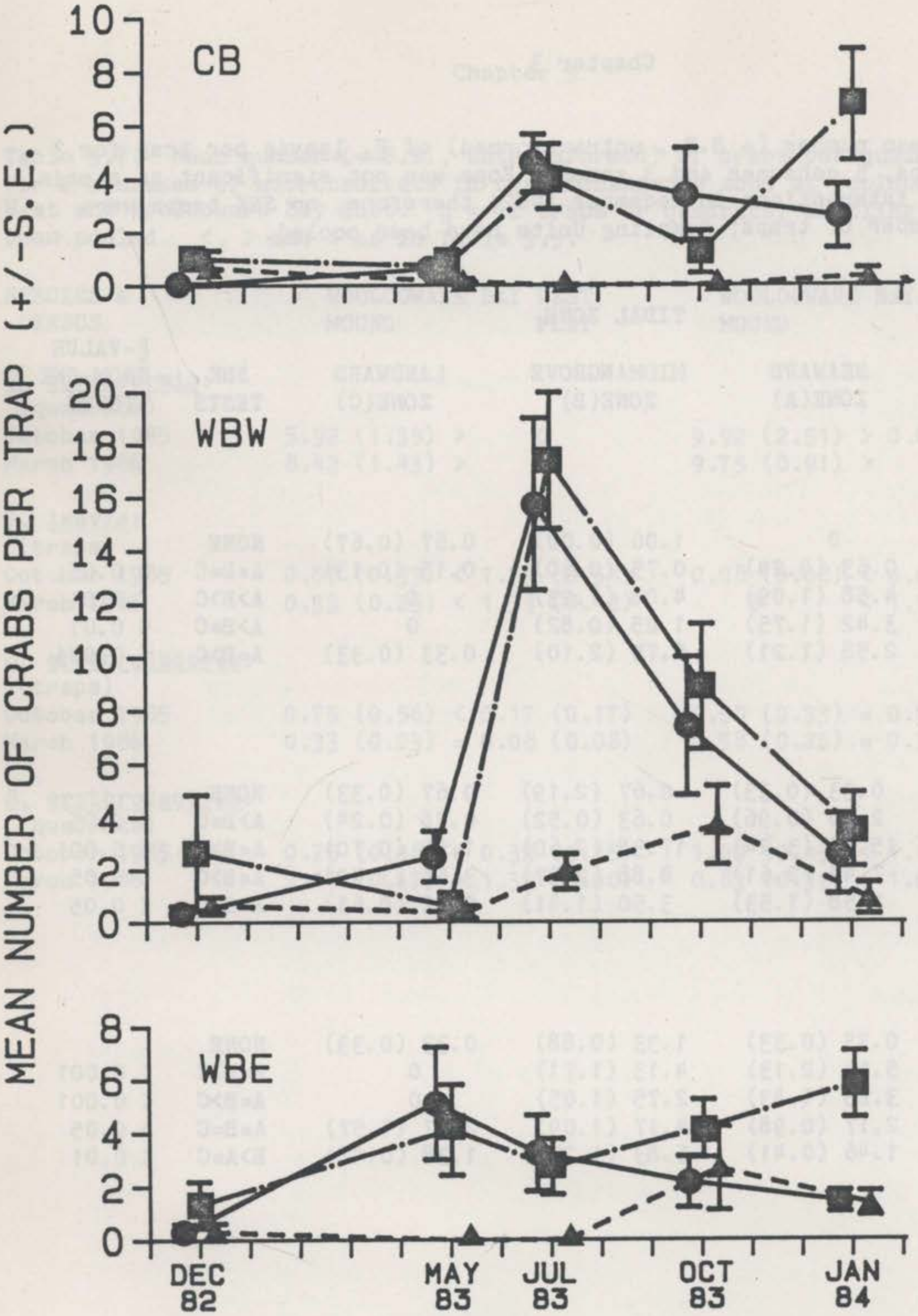

Figure 3.4. Mean number (+/- S.E.) of P. laevis per trap, for 3 mangrove swamps and 3 zones. CB = Careel Bay, WBW = Woolooware Bay West, and WBE = Woolooware Bay East. Circles = seaward zone, squares = midmangrove zone, and triangles = landward zone.

between these two zones was variable. In 6 of 12 SNK tests (3 mangroves x 4 censuses), the mean numbers of crabs per trap in the seaward zone were similar to those in the midmangrove zone. In 3 comparisons, crabs were significantly more abundant in the seaward zone than either the midmangrove or shoreward zones. In one comparison, crabs were more abundant in the midmangrove zone than the zones above or below it on the shore (Table 3.8). The 2 remaining comparisons showed a non-significant but similar pattern to this third relationship.

Because swamps were censused quarterly, preliminary analyses of seasonal effects on zonal patterns could be done. A rigorous test of seasonal effects would, however, require replication over several years. At Woolooware Bay West, only two zonal patterns were observed in the four censuses of P. laevis: 1) in autumn (May 1983), significantly more crabs were caught in traps in the seaward zone than in the two upper zones and 2) in the other three seasons, significantly more crabs were caught in the lower two zones than in the landward zone ($P < 0.05$, Table 3.8). Crabs were generally more abundant in the midmangrove zone than in the seaward zone, except in autumn. Although not specifically examined in this study, other investigations have reported seasonal seaward migrations of ovigerous females (Ono 1959; Warner 1967), and this was thought a possible explanation for the greater numbers of crabs in the seaward zone in autumn. Although the greatest proportion of female crabs in the seaward zone did occur in autumn (Appendix 3.4), all three zones had the greatest proportion of females at this time and SNK tests did not indicate a significantly greater proportion of females in the seaward zone in autumn relative to other times of the year. Additionally, no greater proportion of females in the lower zone(s) occurred in autumn in the other

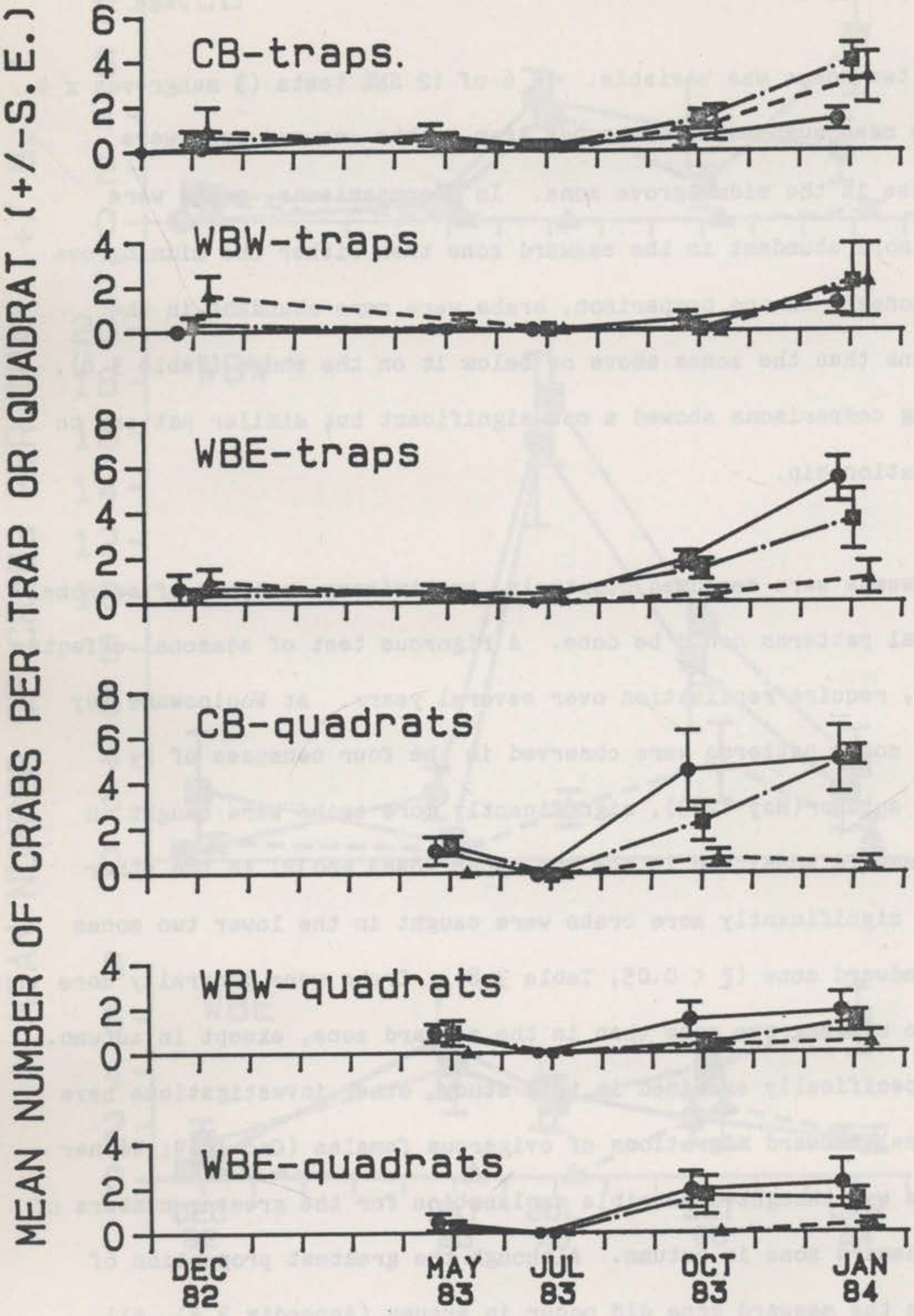

Figure 3.5. Mean number (+/- S.E.) of S. erythrodactyla per trap or quadrat, for 3 mangrove swamps and 3 zones. CB = Careel Bay, WBW = Woolooware Bay West, and WBE = Woolooware Bay East. Circles = seaward zone, squares = midmangrove zone, and triangles = landward zone.

two swamps (Woolooware Bay East and Careel Bay). Migration of females is, therefore, not a likely explanation for the observed greater abundance of crabs in the seaward zone compared with the midmangrove zone in the May 1983 census.

The zonal patterns of abundance were different for three of the four censuses at Wolooware Bay West and for all censuses at Woolooware Bay East. The patterns for each census were different between these two areas and, therefore, the variability in zonal patterns is not explicable by consistent differences among seasons.

In the midmangrove zone at Careel Bay, P. laevis occurred in burrows predominantly in flat areas of the substratum (SNK tests; P < 0.001; Table 3.5; Figure 3.3). The only census not consistent with this pattern was October 1983, when few crabs of any species were trapped. Also, few crabs were trapped in the landward zone (Table 3.6). These data indicated no significant difference in the abundance of crabs between mounds and flats.

At Woolooware Bay West and Woolooware Bay East, P. laevis was always significantly more abundant in flat areas than in mounds (Table 3.7). The distributional pattern of this species, therefore, was consistent among swamps and among seasons.

3. S. erythrodactyla

In contrast to the prevalence of zonal differences in the distribution of P. laevis, S. erythrodactyla was usually trapped in similar numbers among all three zones, regardless of swamp or season (Figure 3.5). Only 2 of 12

Table 3.9. Mean number (+ S.E., untransformed) of _S. erythrodactyla_ per trap for 3 mangrove swamps, 5 censuses and 3 zones. Zone was not significant as a main effect or in interactions in December 1982; therefore, no SNK tests were done. _n_ = number of traps; Sampling Units have been pooled.

	TIDAL ZONE				
MANGROVE & CENSUS (_n_)	SEAWARD ZONE(A)	MIDMANGROVE ZONE(B)	LANDWARD ZONE(C)	SNK TESTS	_P_-VALUE FROM SNK TESTS
Careel Bay:					
Dec 82 (3)	1.33 (0.88)	0.67 (0.33)	1.00 (1.00)	NONE	
May 83 (8)	0.75 (0.50)	0.50 (0.37)	0.25 (0.25)	A=B=C	> 0.05
July 83 (12)	0.25 (0.25)	0.25 (0.25)	0.08 (0.08)	A=B=C	> 0.05
Oct 83 (12)	0.60 (0.42)	1.42 (0.42)	1.25 (0.78)	A=B=C	> 0.05
Jan 84 (12)	1.42 (0.47)	4.00 (0.80)	3.25 (1.15)	A=B=C	> 0.05
Woolooware Bay West:					
Dec 82 (3)	0	0.33 (0.33)	1.67 (0.88)	NONE	
May 83 (8)	0.13 (0.13)	0.13 (0.13)	0.50 (0.29)	A=B=C	> 0.05
July 83 (12)	0	0.08 (0.08)	0.08 (0.08)	A=B=C	> 0.05
Oct 83 (12)	0.50 (0.39)	0.08 (0.08)	0.08 (0.08)	A=B=C	> 0.05
Jan 84 (12)	1.25 (0.52)	2.25 (1.67)	2.25 (1.06)	A=B=C	> 0.05
Woolooware Bay East:					
Dec 82 (3)	0.67 (0.67)	0.33 (0.33)	1.00 (0.58)	NONE	
May 83 (8)	0.50 (0.35)	0.38 (0.24)	0.25 (0.25)	A=B=C	> 0.05
July 83 (12)	0	0.42 (0.25)	0	A=B=C	> 0.05
Oct 83 (12)	1.92 (0.39)	1.50 (0.47)	0.33 (0.33)	A=B>C	< 0.05
Jan 84 (12)	5.42 (1.01)	3.67 (1.32)	1.08 (0.73)	A=B>C	< 0.01

analyses indicated a significant difference among zones: at Woolooware Bay East, in October 1983 and January 1984, this species was significantly more abundant in the lower two zones (Table 3.9).

Results of analyses of data from quadrats were fairly similar to those from traps in all swamps in May and October 1983: S. erythrodactyla was similarly abundant in all zones (Table 3.10; Figure 3.5). In January 1984, however, crabs were significantly more abundant in the lower two zones.

Comparison of graphs of data from quadrats versus traps (Figure 3.5) suggests differences between these two methods of sampling. These differences are not surprising in that traps sample crabs moving across the substratum during a 48-hour period whereas quadrats sample crabs emerging from burrows in a restricted area (0.25 m^2) during a 10-minute period. The analyses from both methods, however, generally indicate that S. erythrodactyla occurred in similar abundances among zones although in spring and summer there may have been a slight tendency for greater abundances in the lower two zones.

Too few S. erythrodactyla were collected to examine the effect of season on proportion of females in each zone (to assess the possibility of seaward reproductive migration of females). The only striking and consistent seasonal effect was the almost complete absence of this species from the surface of the substratum during winter (July 1983).

In the midmangrove zone at Careel Bay, similar numbers of S. erythrodactyla were found in mounds and flats in 5 of 7 SNK tests (Table 3.5;

Table 3.10. Mean number (+ S.E., untransformed) of *S. erythrodactyla* per quadrat for 3 mangrove swamps, 3 censuses and 3 zones. Sampling by quadrats was not done in the census of December 1982. Because few crabs were seen in July 1983, no analysis of variance was done for this census. *n* = number of quadrats; Sampling Units have been pooled.

		TIDAL ZONE			
MANGROVE & CENSUS (*n*)	SEAWARD ZONE(A)	MIDMANGROVE ZONE(B)	LANDWARD ZONE(C)	SNK TESTS	P-VALUE FROM SNK TESTS
Careel Bay:					
May 83 (8)	1.00 (0.63)	1.20 (0.44)	0	A=B=C	> 0.05
Oct 83 (12)	4.50 (1.78)	2.25 (0.85)	0.67 (0.39)	A=B=C	> 0.05
Jan 84 (12)	5.00 (1.48)	5.17 (0.46)	0.42 (0.31)	A=B>C	< 0.001
Woolooware Bay West:					
May 83 (8)	0.90 (0.41)	0.90 (0.57)	0	A=B=C	> 0.05
Oct 83 (12)	1.50 (0.76)	0.42 (0.42)	0.33 (0.25)	A=B=C	> 0.05
Jan 84 (12)	1.83 (0.89)	1.42 (0.48)	0.50 (0.50)	A=B>C	< 0.05
Woolooware Bay East:					
May 83 (8)	0.50 (0.39)	0.30 (0.30)	0.10 (0.10)	A=B=C	> 0.05
Oct 83 (12)	1.92 (0.81)	1.67 (0.87)	0	A=B=C	> 0.05
Jan 84 (12)	2.17 (1.07)	1.50 (0.50)	0.42 (0.23)	A=B>C	< 0.001

Figure 3.3). The two remaining censuses indicated significantly more crabs were trapped in mounds than in flats. In the landward zone, S. erythrodactyla were evenly distributed between mounds and flats (Table 3.6).

At Woolooware Bay West and Woolooware Bay East, S. erythrodactyla was found with similar frequency in both microhabitats in 4 of 8 analyses, with greater frequency in mounds in 3 analyses and with greater frequency in flats in one analysis (Table 3.7). This species, therefore, tended to be evenly distributed between mounds and flats in all three swamps. When differences occurred, these generally indicated greater abundance in mounds than in flats. These patterns did not vary in any consistent way among seasons.

Discussion

Two general trends are possible with respect to tidal heights on the shore: 1) crabs might show distinct zonal patterns, wherein a given species is consistently more abundant in one or more zones than the others or 2) at best, crabs might show general tendencies to be more abundant high or low on the shore. Studies in which the mangrove is divided into many zones would tend to yield results consistent with the second trend (e.g. McCormick 1978 found only general trends among 5 zones in mangrove swamps near Sydney), because the differences between adjacent zones would become smaller if a larger number of fine divisions were made. In this study, the decision to divide mangroves into only three broad zones was made to amplify differences between zones, should such zonal patterns be a real phenomenon. Despite this larger scale of division, species-specific zonal patterns, when present, suggested only general trends: H. cordiformis were usually more abundant in the midmangrove zone; P. laevis tended to be more abundant in the seaward zone; whereas S. erythrodactyla was distributed fairly evenly among all three zones.

These patterns were similar to those found by Yates (1978) at Patonga (60 km north of Sydney) and McCormick (1978) in 6 mangrove swamps scattered widely along the coast of New South Wales, except that in the latter study, P. laevis was most abundant in the upper midmangrove and shoreward zones.

Several studies on crabs in estuaries or mangrove swamps have found a relationship between zonal patterns and taxonomic family. Investigations of mangrove swamps in Malaysia (Berry 1963, 1972; Sasekumar 1974) and in Thailand (Frith et al. 1976) all showed that grapsids were most common high on the shore and that ocypodids were most abundant lower on the shore. The findings of Griffin (1971), Macnae (1967), Snelling (1959) and this study indicate that zonal patterns in mangrove swamps along the east coast of Australia are less marked and in many cases inconsistent with this proposed familial pattern. For example, the two grapsids in this study (P. laevis and S. erythrodactyla) tended to be most abundant low on the shore whereas H. cordiformis (an ocypodid) tended to be most abundant in the midmangrove or seaward zone.

No assessment of zonal patterns could be made for H. cordiformis during the census in July 1983 because few crabs emerge onto the surface of the substratum during winter. This situaton, that crabs may be present but not amenable to sampling, raises a very important question with respect to the nature (meaning) of the data collected by traps and quadrats. Unless every crab present in a given volume of substratum can be accurately censused, true 'abundances' can not be determined. There is no accurate method for censusing the number of crabs in a volume of mud. One limitation concerns probable adverse effects on the swamp. Digging up and breaking apart clumps of substratum causes long-term damage to the mangrove swamp: the network of peg roots and nutritive roots which consolidate the otherwise oozy soils may take many years to reform and regenerate to a state comparable to undisturbed sites. Even when exhumed substratum was replaced, the hole remained a sink of loose mud throughout the three years of this study, with little sign of recovery.

Large scale damage would have resulted if crabs were censused in this way, on a scale similar to that used for traps and quadrats. Not only would this have been an unethical abuse of the habitat, but such damage would have greatly altered the nature of the substratum and this, in turn, may have affected the suitability of these areas for subsequent occupation by crabs. Because the focus of this study was on the distributional patterns of crabs, methods of sampling were chosen which would minimise altering the natural distributions of the experimental animals.

A number of chemicals ranging in toxicity from distilled water to petrol, were tested for the effectiveness in inducing crabs to emerge from burrows. None proved even remotely successful. Even if one or more of these substances had proven effective, they might have had persistent effects and might have altered the suitability of the substratum for subsequent inhabitants.

Despite this inability to determine actual abundances, determination of distributional patterns by the use of traps and quadrats was based upon a subset of the population of each species: crabs active on the surface of the mangrove swamp during low tide (i.e. 'apparent' abundance). The only potential problem with ascertaining patterns on the basis of this subset is that crabs in their burrows may be distributed differently. This is unlikely for several reasons. For H. cordiformis, the majority of behaviours (e.g. feeding, attraction of mates, defence) are all performed near their burrows (Griffin 1968; pers. observation); therefore, the distribution of crabs, as determined by the number of H. cordiformis emerging from their burrows and remaining within quadrats, indeed represents the distribution of these crabs in their burrows. The fidelity of the other two species to their burrows is less certain. S. erythrodactyla and P. laevis wander further from their burrows (pers. observation) and, within the 10-15 minute periods of observation in this study, only rarely returned to the same burrow.

Data from traps (mainly S. erythrodactyla and P. laevis) most certainly represent crabs moving over the surface. The predominance of P. laevis in the lower two zones, therefore, could indicate 1) where they inhabit burrows, 2) where they spend the majority of the period of low tide, or 3) where they go to feed. The first two possibilities do not affect the validity of the zonal patterns described in this chapter. The third possibility would suggest that P. laevis observed during low tide should be moving seaward soon after low tide (a well-documented observation for feeding-herds of fiddler crabs, Crane 1975). No such migration was ever observed during this study nor in other studies on crabs in mangroves in New South Wales (McCormick 1978; Yates 1978).

Were the distributional pattern of S. erythrodactyla determined from traps only, the general lack of zonation may have been merely a consequence of large-scale movements of crabs across zones. This would have the effect of masking a zonal pattern with respect to occupancy of burrows. Weakening that possibility, however, were similar results from quadrats, which sampled crabs as they emerged from burrows.

With the exception of data from quadrats for S. erythrodactyla, variations in distributional patterns among zones did not vary in any consistent way among censuses. There was, therefore, no justification for suggesting that variability in patterns for P. laevis or H. cordiformis was due to seasonal environmental changes. Season may have had an effect on the zonal patterns of S. erythrodactyla seen in quadrats because in January 1984, in all three swamps, this species became significantly more abundant in the lower zones. Summer is the breeding season for S. erythrodactyla (Yates 1978), and ovigerous females may migrate to the seaward zone to disperse hatching larvae. Such reproductive migrations, from high to low areas on the shore have been reported for at least two intertidal crabs: Aratus pisoni (Warner 1967) and Sesarma haematocheir (Ono 1959) but was not specifically examined in the present study.

In 4 of 8 analyses of variance, the mean numbers of crabs sampled varied amongst the different mangrove swamps; in 3 other analyses the interaction of Mangrove with Zone was significant (Table 3.1). Physical and chemical differences among swamps (e.g. compactability of soils, distribution of particle sizes of sediments, etc.) might be correlated with the lack of consistent zonal patterns but were not examined in this study.

Analyses of the distributional patterns of the three species of crabs in mounds and flats indicated significant and consistent differences in the occupation of these two microhabitats. McCormick (1978) suggested dissimilar occupation of other types of microhabitats, which was also observed (although not tested) in the present study. S. erythrodactyla and P. laevis, for example, were commonly found under debris on the mangrove surface, in rotting wood, and in oyster clumps. The former species was often seen on the trunks and branches of mangrove trees. Griffin (1971), Snelling (1959), Warner (1969) and others have reported relationships between other species of crabs and a variety of microhabitats (e.g. the grapsid Helice haswellianus was most abundant in substrata covered with stones). Griffin (1971) also suggested that patterns of zonation are less distinct for crabs than for other intertidal organisms such as molluscs and barnacles but that patterns associated with microhabitats are far more consistent. The present study supports this generalisation.

The patterns of distribution of H. cordiformis, P. laevis and S. erythrodactyla between mounds and flats may be the consequence of habitat preferences or interspecific interactions. If the former model is correct for all species, then H. cordiformis is found in mounds and P. laevis is found in flats because each species chooses to occupy burrows in different microhabitats, whereas S. erythrodactyla demonstrates no preference. Alternatively, the activities of one species might displace another from its preferred microhabitat or displace a species with no real preference from a particular microhabitat (i.e. interspecific interference). Interspecific interactions needn't be inhibitory. P. laevis and S. erythrodactyla have never been observed excavating nor maintaining the burrows they occupy.

Perhaps they require another burrowing animal (e.g. H. cordiformis or a callianassid prawn) to provide burrows, and then displace these animals from their residences. These models were examined in subsequent experiments (Chapter 5).

CHAPTER 4. SEASONAL VARIABILITY IN ABUNDANCES, SIZE-FREQUENCY DISTRIBUTIONS, SEX RATIOS AND OCCURRENCE OF OVIGEROUS FEMALES

Introduction

In the previous chapter, seasonal variations in the distributional patterns of crabs among zones and between microhabitats were examined. In this chapter, seasonal effects on overall abundances are examined with the aim of describing when greatest and smallest densities of each species occurred. As in the previous chapter, results and conclusions regarding seasonal effects in these analyses must be considered preliminary, because seasons were not replicated.

Size-frequency distributions of males and females of the three species of crabs were also investigated among seasons and among tidal zones. Sex ratios were recorded throughout the year, and the seasonality of ovigery for each species was examined.

Methods and Materials

Data from traps and quadrats were used as in the previous chapter. Size-frequency distributions, sex ratios and occurrence of ovigerous females of *P. laevis* and *S. erythrodactyla* were recorded from samples in traps. Visual counts of *H. cordiformis* in quadrats did not allow accurate determination of size or identification of ovigerous females. Also, identification of males and females by visual sampling was not always possible when crabs were partially obscured by peg roots or did not emerge completely from the entrance to burrows, or when crabs were too small for dimorphism in size of chelae to allow discrimination between males and females.

Accordingly, *H. cordiformis* were sampled in blocks of substratum (0.5 m x 0.5 m x 0.3 m deep). These were quickly dug up and deposited in large plastic bins to prevent escape of crabs during sorting. Crabs were extracted from the burrows in these blocks by tearing clumps of substratum, peg roots, etc. from the larger block and carefully examining the material for crabs. During the 45-60 minutes needed to process the entire block, many crabs left their damaged burrows and accumulated in the bottom of bins, and were subsequently counted and measured (for carapace length). This method was not biased with respect to sex or reproductive condition of crabs, but an indeterminate number of individuals smaller than 5 mm may have been overlooked. Analyses of abundance, size frequency and sex ratios were, therefore, limited to crabs of at least 5 mm carapace length (measured with calipers). Three blocks of mud were sampled in this manner in each zone of the three swamps in September 1985 (spring), December 1985 (summer) and March 1986 (autumn).

Results

Seasonal variability in abundances

Seasonal differences in abundances were not consistent in all swamps or zones except for *S. erythrodactyla* censused by traps (Table 4.1). In addition, numbers of *H. cordiformis* and *P. laevis* varied significantly (although in no consistent manner) between Sampling Units, indicating differences in abundance between sites within zones and/or consecutive censuses.

Table 4.1. Analyses of variance of the mean numbers of crabs per trap or quadrat during 4 seasons when zones were censused: May 1983 (autumn), July 1983 (winter), October 1983 (spring) and January 1984 (summer). SU = Sampling Unit (see text in Chapter 3 for definition). *n* = 2 Sampling Units, each consisting of 3 traps or 3 quadrats.

A. *H. cordiformis* - QUADRATS. Data were transformed to $\ln(x+1)$, and Cochran's test was not significant ($P > 0.05$).

SOURCE	DF	MS	F	P
Season	3	41.89	69.81	< 0.001
Mangrove	2	0.32	0.53	> 0.50
Zone	2	13.36	22.27	< 0.001
S x MA	6	0.36	0.60	> 0.50
S x Z	6	1.97	3.28	< 0.025
MA x Z	4	4.11	6.85	< 0.001
S x MA x Z	12	1.23	2.05	> 0.05
SU(SxMAxZ)	36	0.60	2.22	< 0.025
Residual	144	0.27		

B. *P. laevis* - TRAPS. Data were transformed to $\ln(x+1)$, and Cochran's test was not significant ($P > 0.05$).

SOURCE	DF	MS	F	P
Season	3	4.32	4.28	< 0.025
Mangrove	2	0.25	0.25	> 0.50
Zone	2	19.67	19.48	< 0.001
S x MA	6	6.48	6.42	< 0.001
S x Z	6	1.40	1.39	> 0.10
MA x Z	4	0.69	0.68	> 0.50
S x MA x Z	12	0.87	0.86	> 0.25
SU(SxMAxZ)	36	1.01	3.61	< 0.001
Residual	144	0.28		

C. *S. erythrodactyla* - TRAPS. Data were transformed to $x^{0.25}$, and Cochran's test was not significant ($P > 0.05$).

SOURCE	DF	MS	F	P
Season	3	6.84	18.49	< 0.001
Mangrove	2	0.06	0.16	> 0.50
Zone	2	0.68	1.84	> 0.10
S x MA	6	0.84	2.27	> 0.10
S x Z	6	0.21	0.57	> 0.50
MA x Z	4	0.78	2.11	> 0.10
S x MA x Z	12	0.28	0.76	> 0.50
SU(SxMAxZ)	36	0.37	1.61	> 0.05
Residual	144	0.23		

Table 4.1. (Cont'd.)

D. S. erythrodactyla - QUADRATS. Data were transformed to ln (x+1), and Cochran's test was not significant ($P > 0.05$).

SOURCE	DF	MS	F	P
Season	3	7.41	52.93	< 0.001
Mangrove	2	1.67	11.93	< 0.001
Zone	2	3.96	28.29	< 0.001
S x MA	6	0.75	5.36	< 0.001
S x Z	6	0.62	4.43	< 0.005
MA x Z	4	0.30	2.14	> 0.05
S x MA x Z	12	0.32	2.29	< 0.05
SU(SxMAxZ)	36	0.14	0.74	> 0.50
Residual	144	0.19		

Table 4.2. Mean number (+ S.E., untransformed) of *H. cordiformis* per quadrat during 4 seasons when zones were censused. *n* = 6 quadrats; Sampling Units within each zone have been pooled. SNK tests were done at the *P* = 0.05 level.

MANGROVE & ZONE	AUTUMN 83	WINTER 83	SPRING 83	SUMMER 84	SNK TESTS
Careel Bay:					
Seaward	0.83 (0.67)	0	3.00 (1.22)	5.50 (1.47)	AU=WI=SP=SU
Midmangrove	12.50 (1.04)	0	9.67 (2.03)	10.00 (1.43)	WI<AU=SP=SU
Landward	5.17 (2.72)	0	2.33 (0.77)	5.17 (1.97)	WI<AU=SP=SU
Woolooware Bay West:					
Seaward	16.67 (5.73)	0	7.00 (1.34)	8.84 (3.77)	WI<AU=SP=SU
Midmangrove	10.33 (1.33)	0	9.00 (1.10)	10.50 (2.36)	WI<AU=SP=SU
Landward	3.17 (0.60)	0	2.17 (1.09)	3.50 (0.89)	AU=WI=SP=SU
Woolooware Bay East:					
Seaward	0.67 (0.17)	0	2.83 (1.48)	3.33 (2.63)	AU=WI=SP=SU
Midmangrove	8.33 (1.10)	0	10.33 (2.64)	16.50 (2.40)	WI<AU=SP=SU
Landward	9.50 (1.94)	0	2.83 (1.33)	7.17 (0.67)	WI<AU=SP=SU

Except for winter, the numbers of H. cordiformis did not differ significantly among seasons (Table 4.2). The greatest densities in each swamp were found in autumn (May 1983) in the midmangrove zone at Careel Bay, in autumn (May 1983) in the seaward zone at Woolooware Bay West and in summer (January 1984) in the midmangrove zone at Woolooware Bay East.

In all zones at Careel Bay, P. laevis was most abundant in spring (October 1983), but at Woolooware Bay West was most abundant in winter (July 1983; Table 4.3). Differences in abundances among seasons were generally smaller at Woolooware Bay East and were not consistent among zones.

In general, the numbers of S. erythrodactyla caught in traps varied little among seasons, except at Careel Bay where greatest abundances occurred in summer (January 1984; Table 4.4). Data from quadrats indicated than when differences occurred, crabs were usually more abundant in spring and summer than in autumn or winter (Table 4.5).

Size-frequency distributions

Changes in size frequency distributions were inconsistent but useful for examination of the relationships between i) size and sex and ii) size and zone.

1. H. cordiformis

Most comparisons between males and females suggested no difference in size between the sexes (Figure 4.1). The size of each sex increased with increasing tidal height on the shore. This pattern was consistent among the three seasons when this species was sampled.

Table 4.3. Mean number (+ S.E., untransformed) of P. laevis per trap during 4 seasons when zones were censused. n = 6 traps; Sampling Units within each zone have been pooled. SNK tests were done at the P = 0.05 level.

MANGROVE & ZONE	AUTUMN 83	WINTER 83	SPRING 83	SUMMER 84	SNK TESTS
Careel Bay:					
Seaward	0.83 (0.17)	3.83 (0.88)	6.00 (2.53)	2.50 (0.90)	AU=WI=SP=SU
Midmangrove	0.67 (0.44)	3.00 (0.76)	11.00 (4.03)	5.50 (1.37)	AU=WI=SP=SU
Landward	0	0	2.83 (1.37)	0.67 (0.67)	AU=WI=SP=SU
Woolooware Bay West:					
Seaward	2.00 (1.10)	19.00 (3.47)	4.67 (2.06)	3.00 (1.76)	AU=SP=SU<WI
Midmangrove	0.83 (0.67)	18.67 (3.61)	0.33 (0.33)	3.00 (0.89)	AU=SP=SU<WI
Landward	0.50 (0.29)	2.83 (0.61)	0	0.67 (0.45)	AU=WI=SP=SU
Woolooware Bay East:					
Seaward	5.67 (2.91)	4.00 (1.37)	2.17 (0.94)	0.61 (0.50)	AU=WI=SP=SU
Midmangrove	4.33 (2.00)	2.67 (1.37)	3.83 (0.83)	6.33 (1.42)	AU=WI=SP=SU
Landward	0	0	1.67 (0.46)	2.00 (0.50)	AU=WI=SP=SU

Table 4.4. Mean number (+ S.E., untransformed) of _S. erythrodactyla_ per trap during 4 seasons when zones were censused. _n_ = 6 traps; Sampling Units within each zone have been pooled. SNK tests were done at the _P_ = 0.05 level.

MANGROVE & ZONE	AUTUMN 83	WINTER 83	SPRING 83	SUMMER 84	SNK TESTS
Careel Bay:					
Seaward	0.83 (0.61)	0.17 (0.17)	0.83 (0.63)	1.83 (0.44)	AU=WI=SP=SU
Midmangrove	0.67 (0.46)	0.33 (0.33)	0.17 (0.17)	4.67 (0.77)	AU=WI=WP<SU
Landward	0.33 (0.33)	0.17 (0.17)	0	2.67 (1.21)	AU=WI=SP<SU
Woolooware Bay West:					
Seaward	0.17 (0.17)	0	0.83 (0.33)	1.17 (0.17)	AU=WI=SP=SU
Midmangrove	0	0.17 (0.17)	1.17 (0.33)	3.00 (2.56)	AU=WI=SP=SU
Landward	0.33 (0.33)	0.17 (0.17)	1.50 (0.79)	2.17 (0.62)	AU=WI=SP=SU
Woolooware Bay East:					
Seaward	0.17 (0.17)	0	2.33 (0.17)	4.67 (1.17)	AU=WI=SP=SU
Midmangrove	0.50 (0.29)	0.50 (0.33)	2.00 (0.61)	3.33 (1.87)	AU=SI=SP=SU
Landward	0.33 (0.33)	0	0.33 (0.33)	1.17 (1.17)	AU=WI=SP=SU

Table 4.5. Mean number (+ S.E., untransformed) of *S. erythrodactyla* per quadrat during 4 seasons when zones were censused. *n* = 6 quadrats; Sampling Units within each zone have been pooled. SNK tests were done at the *P* = 0.05 level.

MANGROVE & ZONE	AUTUMN 83	WINTER 83	SPRING 83	SUMMER 84	SNK TESTS
Careel Bay:					
Seaward	0.33 (0.33)	0	4.33 (1.77)	3.83 (0.61)	AU=WI<SP=SU
Midmangrove	1.17 (0.67)	0	2.17 (1.03)	4.17 (0.46)	WI<AU<SP<SU
Landward	0	0	1.00 (0.61)	0.33 (0.33)	AU=WI=SP=SU
Woolooware Bay West:					
Seaward	1.00 (0.57)	0	0.83 (0.46)	2.00 (1.06)	WI<AU=SP=SU
Midmangrove	1.00 (0.83)	0	0.50 (0.50)	1.33 (0.46)	AU=WI=SP=SU
Landward	0	0	0.33 (0.17)	0.50 (0.50)	AU=WI=SP=SU
Woolooware Bay East:					
Seaward	0.83 (0.60)	0	1.17 (0.96)	1.50 (0.61)	AU=WI=SP=SU
Midmangrove	0.33 (0.33)	0	1.67 (1.02)	1.67 (0.50)	AU=WI<SP=SU
Landward	0.17 (0.17)	0	0	0.83 (0.46)	AU=WI=SP=SU

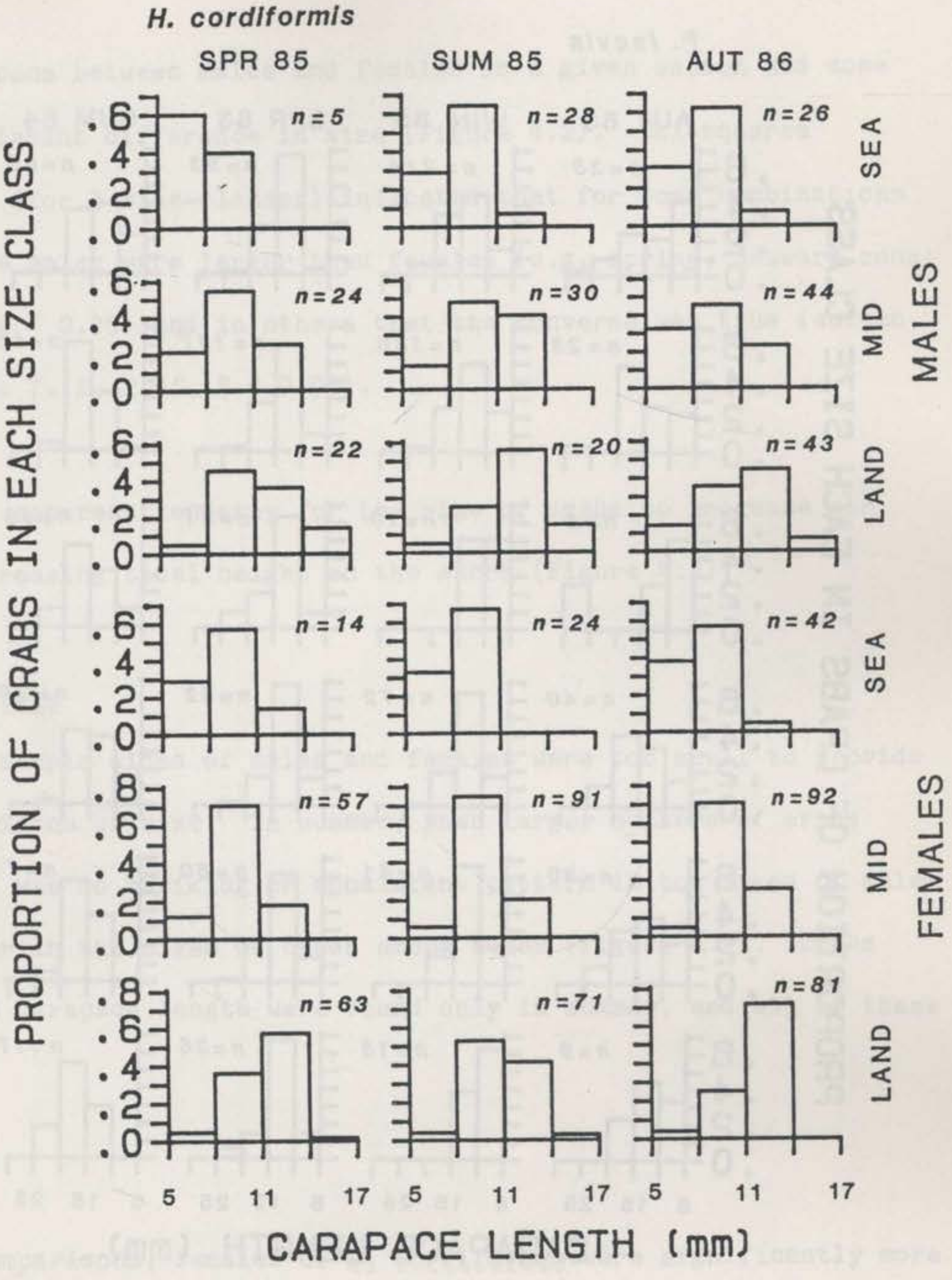

Figure 4.1. Size-frequency distributions of male and female H. cordiformis in 3 seasons. Data from 3 swamps and all Sampling Units (within each zone) have been pooled. n = number of crabs. SEA = seaward zone, MID = midmangrove zone, and LAND = landward zone.

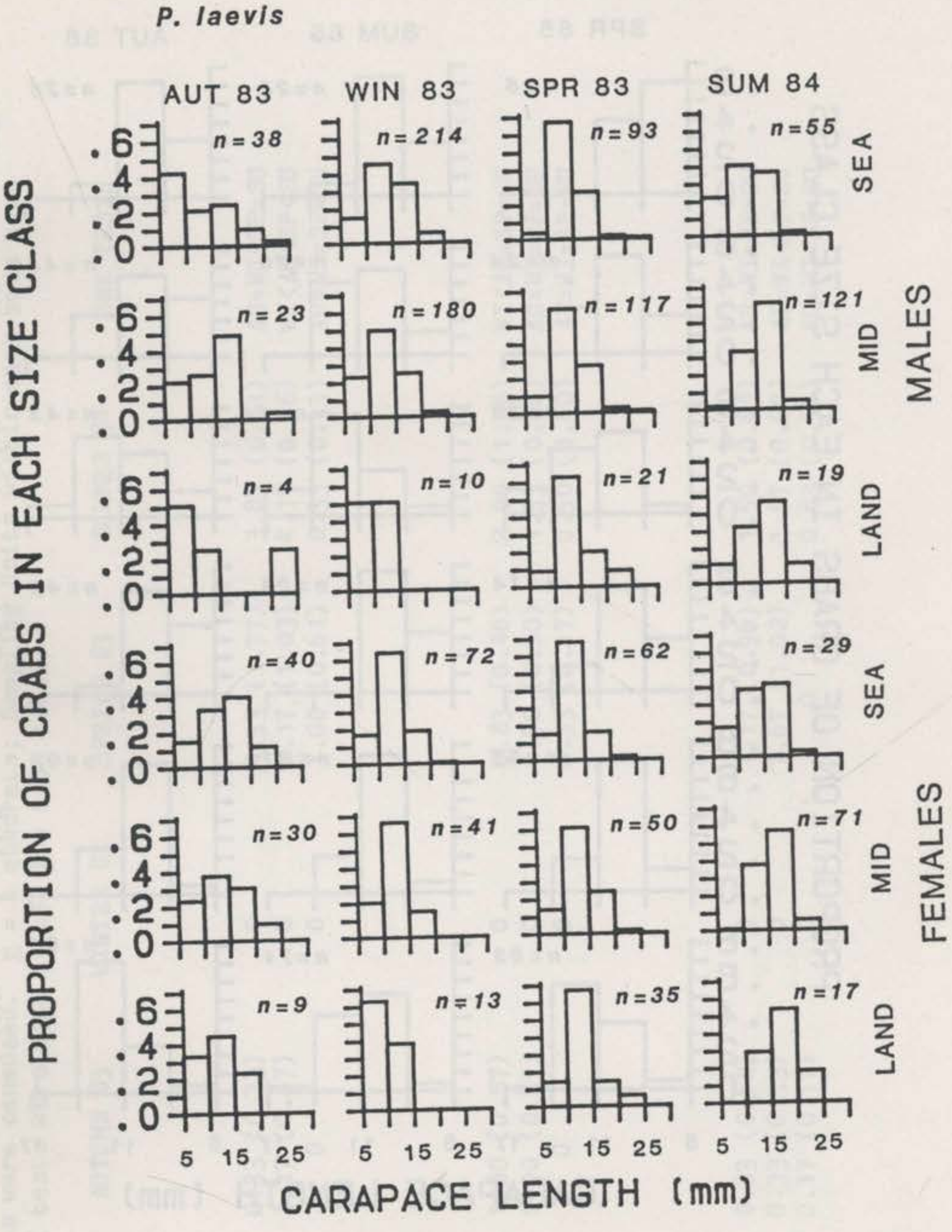

Figure 4.2. Size-frequency distributions of male and female P. laevis in 4 seasons. Data from 3 swamps and all Sampling Units (within each zone) have been pooled. n = number of crabs. SEA = seaward zone, MID = midmangrove zone, and LAND = landward zone.

2. *P. laevis*

Most comparisons between males and females in a given season and zone suggested no consistent difference in size (Figure 4.2). Chi-squared contingency tests (for 3 size-classes) indicated that for some combinations of season and zone males were larger than females (e.g. spring, seaward zone: $\chi^2 = 6.92$, 2 df, $P < 0.05$) and in others that the converse was true (autumn, seaward zone: $\chi^2 = 7.12$, 2 df, $P < 0.05$).

There was no apparent tendency for the size of crabs to increase nor decrease with increasing tidal height on the shore (Figure 4.2).

3. *S. erythrodactyla*

In general, sample sizes of males and females were too small to provide meaningful comparisons of size. In summer, when larger numbers of crabs were caught, there was no striking or consistent pattern in the sizes of males versus females nor in the sizes of crabs among zones (Figure 4.3). Crabs larger than 15 mm carapace length were found only in summer, and all of these were males.

Sex ratios

In 7 of 9 comparisons, females of *H. cordiformis* were significantly more abundant than males (Table 4.6A). For *P. laevis*, the ratio of males to females varied among seasons and zones (Table 4.6B). Significant differences between proportions of males and females occurred only in the seaward and midmangrove zones where males outnumbered females in winter, spring and summer. The disparity in the abundance of males versus females was greatest in winter. In autumn, in these two zones, crabs did not depart from a 1:1

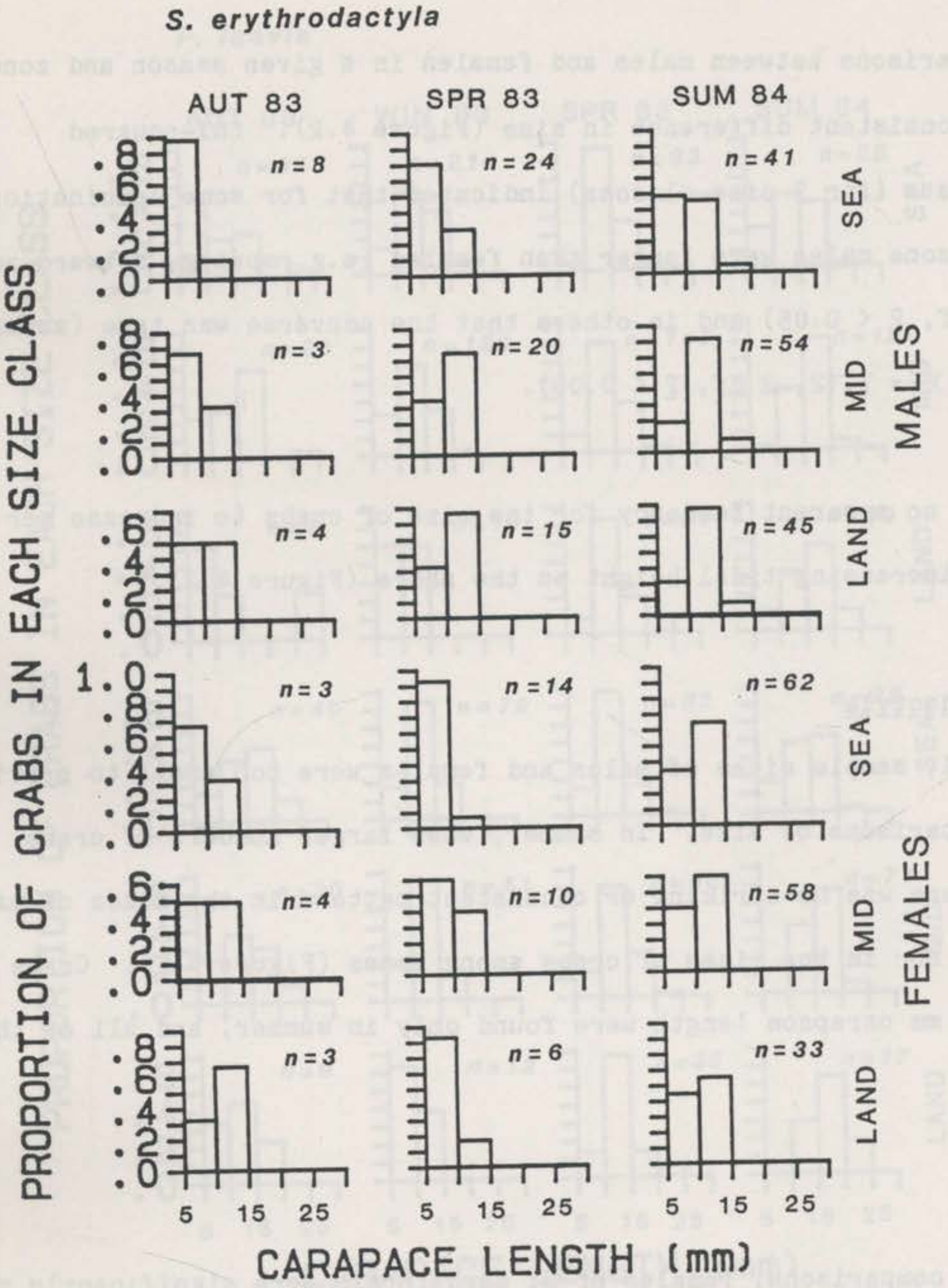

Figure 4.3. Size-frequency distributions of male and female S. erythrodactyla in 3 seasons. Data from 3 swamps and all Sampling Units (within each zone) have been pooled. n = number of crabs. SEA = seaward zone, MID = midmangrove zone, and LAND = landward zone.

Table 4.6. Sex ratios (male:female) of *H. cordiformis*, *P. laevis* and *S. erythrodactyla* in 3 zones and in 3-4 seasons. Data from 3 swamps and Sampling Units within each zone have been pooled. *P*-values below sex ratios = probability from chi-squared tests of a 1:1 ratio (with 1 df). (*n*) = number of crabs in each sample.

A. *H. cordiformis* (sampling was not done in winter)

ZONE	SPRING 85	SUMMER 85	AUTUMN 86	*P* FOR χ^2 OF HETEROGENEITY (2 DF)
Seaward	0.36 (19)	1.17 (52)	0.62 (68)	
P	< 0.05	> 0.50	> 0.05	> 0.05
Midmangrove	0.42 (81)	0.33 (121)	0.48 (136)	
P	< 0.001	< 0.001	< 0.001	> 0.25
Landward	0.35 (85)	0.22 (91)	0.53 (124)	
P	< 0.001	< 0.001	< 0.001	> 0.10

B. *P. laevis*

ZONE	AUTUMN 83	WINTER 83	SPRING 83	SUMMER 84	*P* FOR χ^2 OF HETEROGENEITY (3 DF)
Seaward	0.95 (78)	2.97 (286)	1.50 (155)	1.90 (84)	
P	> 0.75	< 0.001	< 0.025	< 0.005	< 0.001
Midmangrove	0.77 (53)	4.39 (221)	2.34 (167)	1.70 (192)	
P	> 0.25	< 0.001	< 0.001	< 0.001	< 0.001
Landward	0.44 (13)	0.77 (23)	0.60 (56)	1.12 (36)	
P	> 0.10	> 0.50	> 0.05	> 0.50	> 0.25

C. *S. erythrodactyla* (very few crabs were caught in winter)

ZONE	AUTUMN 83	SPRING 83	SUMMER 84	*P* FOR χ^2 OF HETEROGENEITY
Seaward	2.67 (11)	1.71 (38)	0.67 (103)	
P	>0.10	> 0.10	< 0.05	< 0.025 (2 df)
Midmangrove	0.75 (7)	2.00 (30)	0.93 (112)	
P	--	> 0.05	> 0.50	> 0.05 (1 df)
Landward	1.33 (7)	2.50 (21)	1.36 (78)	
P	--	< 0.05	> 0.10	> 0.50 (1 df)

Table 4.7. Proportion of females that were ovigerous in each season sampled Data from 3 swamps and Sampling Units within each zone have been pooled. (*n*) = total number of females in each sample.

A. *H. cordiformis* (sampling was not done in winter)

ZONE	SPRING 85	SUMMER 85	AUTUMN 86
Seaward	0.57 (14)	0.33 (24)	0.74 (42)
Midmangrove	0.46 (57)	0.05 (91)	0.88 (92)
Landward	0.13 (63)	0 (71)	0.70 (81)

B. *P. laevis*

ZONE	AUTUMN 83	WINTER 83	SPRING 83	SUMMER 84
Seaward	0.03 (40)	0.31 (72)	0.02 (62)	0 (29)
Midmangrove	0 (30)	0.02 (41)	0 (50)	0 (71)
Landward	0 (9)	0 (13)	0 (35)	0 (17)

C. *S. erythrodactyla* (only 3 females were caught in winter)

ZONE	AUTUMN 83	SPRING 83	SUMMER 84
Seaward	0 (3)	0 (14)	0.08 (62)
Midmangrove	0 (4)	0 (10)	0.07 (58)
Landward	0 (3)	0 (6)	0.06 (33)

ratio. Differences among the four seasons were significant (tests of heterogeneity, Table 4.6B). In the landward zone, there was no departure from a ratio of 1:1 in any season and no variation in sex ratios among seasons.

Five out of 7 analyses demonstrated no difference in the relative abundances of males and females of S. erythrodactyla (Table 4.6C). Females were more abundant than males in summer in the seaward zone, but males outnumbered females in spring in the landward zone. Thus, a 1:1 ratio of males to females was the general pattern for this species.

Occurrence of ovigerous females

In spring, summer and autumn, ovigerous H. cordiformis were found, with the greatest proportions in the last of these seasons (Table 4.7A). Samples with the smallest proportions of ovigerous females were those from the midmangrove and landward zones in summer, when only 5% of the females from the former zone and no females from the latter zone were carrying eggs. Although this species is not active on the surface during winter, hibernating females may be ovigerous. Unfortunately, samples were not collected during this season and, therefore, this possibility could not be examined.

In four seasons when P. laevis were collected, the greatest proportion of ovigerous females occurred in winter, in the seaward zone, when 31% of the females collected were carrying eggs (Table 4.7B). Small numbers of ovigerous females (2-3%) were found in autumn and spring (in the seaward zone) and in winter (in the midmangrove zone). Ovigerous crabs were not found in summer nor in the landward zone.

Ovigerous S. erythrodactyla were found only in summer (January 1984), when 6-8% of the females collected from each zone had external egg masses (Table 4.7C). The relatively small numbers of females that were collected in autumn and spring, however, cannot preclude the possibility that ovigerous females occurred in these seasons.

Discussion

Analyses of distributional patterns (Chapter 3) have already established that abundances vary considerably among several scales of space and time. Results from this chapter indicated a similar lack of consistent patterns among zones and times of sampling. The following discussion relates the patterns (or lack thereof) in this study to those found in other studies of these species.

1. H. cordiformis

In general, seasonal variability in the abundance of H. cordiformis in the present study was similar to that observed by Yates (1978) at Patonga. Yates found greatest numbers in summer and autumn, with significantly fewer crabs in winter and spring. At Careel Bay and Woolooware Bay, when significant differences occurred, these indicated fewer crabs in winter than at other times of the year (Table 4.2). It is interesting to note that results between the two studies were similar despite the use of very different sampling methods - traps by Yates and visual counts of crabs in 0.25 m^2 quadrats in the present study. This supports the usefulness of data from traps (which sample only crabs moving along the surface) in estimating abundances of crabs at or within their burrows.

In addition to sampling *H. cordiformis* from traps (which yielded only 87 crabs from the 13 monthly samples collected), Yates (1978) estimated abundances by photographic censuses of 0.25 m^2 quadrats. These data were (not surprisingly) more similar to those of the present study than his data from traps. Data from photographic censuses at Patonga indicated significantly more crabs in autumn, spring and summer than in winter.

When Yates (1978) pooled samples of *H. cordiformis* from all sampling periods and zones (i.e. $n = 87$ crabs), he found significantly more males than females ($\chi^2 = 19.32$, $P < 0.01$; sex ratio of males/females = 2.8). This contrasts strikingly with ratios from Careel Bay and Woolooware Bay, where females were significantly more abundant than males in 7 of 9 combinations of season and zone (Table 4.6A). The difference between the two studies may reflect spatial variability between Patonga and the swamps sampled here. Another likely explanation is that data from the present study were from visual censuses, which sampled crabs at their burrows and were probably unbiased. Yates' (1978) analyses were, however, based on data from traps, and because males generally wander further from their burrows than females (see Chapter 7), they might more readily fall into traps than females.

Ovigerous *H. cordiformis* were found in samples collected in spring, summer and autumn at Careel Bay, Woolooware Bay West and Woolooware Bay East (except in the landward zone in summer, at this third area; Table 4.7A). The proportions of ovigerous females caught in traps at Patonga were small relative to numbers in the present study (9% in summer, 9% in autumn and 4% in winter, all in the seaward zone at Patonga vs. 33%, 74% and 57% for the corresponding seasons of the present study). Again, this may have been a sampling artifact which represented a tendency of ovigerous females to stay near (or in) their burrows, and hence not fall into traps set by Yates (1978)(see Chapter 7).

In his examination of populations of *H. cordiformis* in eastern Tasmania, Griffin (1971) found ovigerous females only from November through January, although moderate to large samples were collected in all months except October, February and March. Differences between his and the present study could easily be the result of differences between swamps near Sydney versus those far away in Tasmania. Differences arising from different sampling methods could not be assessed because Griffin (1971) did not describe his sampling procedure.

2. *P. laevis*

Yates (1978) found that the abundance of *P. laevis* at Patonga (across Broken Bay from my northernmost site, Careel Bay) did not vary in any consistent manner among seasons, even within a given tidal zone. Analyses of data from the three swamps of my study indicated that significant seasonal effects occured in at least one swamp (Woolooware Bay West, with greatest numbers in winter) and possibly in a second (Careel Bay, with greatest numbers in spring; Table 4.3). The only zone in my study that consistently showed no striking seasonal differences was the landward zone. The differences between results of the two studies are not surprising in light of the variability observed even among the zones within each swamp in the present study. Also, the lack of significant seasonal effects in Yates' (1978) analyses might have resulted from relatively small sample sizes. In his study of Tasmanian populations, Griffin (1971) was able to collect large numbers of P. laevis only in autumn, which corresponds with the peak numbers found during this season at Careel Bay.

The only other study which examined size-frequency distributions of P. laevis was Yates (1978). Because his measurements were of carapace width and mine were of carapace length, and because he pooled results from all seasons, comparisons between the results of our studies are limited to patterns of size relating to zones. In both studies, the most even distribution of crabs in various size-classes occurred in the seaward and midmangrove zones (Figure 4.2). Neither study indicated a significant relationship between size and tidal height on the shore.

When samples from all zones and seasons were pooled, Yates (1978) found no significant difference between the abundance of males and females. When zones were examined separately, a significant difference occurred only in the landward zone where females outnumbered males. Data from the present study, however, indicated that males were significantly more abundant than females in the lower two zones from winter through summer (Table 4.6B). Although differences in the landward zone were not significant, in general they were consistent with the findings of Yates (1978), with more females than males except in summer (when the sex ratio was 1.12). Sex ratios have not been reported elsewhere for P. laevis.

The seasonality of ovigery found in the present study correlates well with that observed by Yates (1978) for the population at Patonga. Both studies found maximum proportions of ovigerous females in winter and smaller numbers in autumn and spring (Table 4.7B). At Patonga and in the three mangrove swamps of the present study, the greatest numbers of ovigerous females were recorded in the seaward zone. Griffin (1971) collected large samples of P. laevis in Tasmania only in spring, but none of these crabs was carrying eggs. During the rest of the year, none of the small numbers of females he collected were ovigerous.

3. S. erythrodactyla

Analyses of abundance of S. erythrodactyla in the present study indicated that numbers varied little among seasons (Tables 4.4 and 4.5). These observations agree with those of Yates (1978). Both studies found that when signficant differences in numbers occurred, this species tended to be most abundant during spring and summer.

Yates (1978) suggested that S. erythrodactyla may be larger in the midmangrove and landward zones than in the seaward zone. Comparisons of zonal patterns in the present study could be made only for summer because sample sizes were too small at other times of the year. No consistent trend was observed for the pooled population from the three study areas at Careel Bay and Woolooware Bay, nor in the data from females alone (Figure 4.3). Males, however, demonstrated a pattern similar to that of Yates (1978), with a greater proportion of larger individuals in the upper two zones.

Yates (1978) found significantly more males than females in all zones when seasons were pooled. Data in the present study suggested similar trends in all zones in spring and in the landward zone in summer, but results of analyses were generally not significant (Table 4.6C). At Patonga, the sex ratio varied consistently among zones, with the greatest bias toward males in the landward zone. In the present study, data from spring and summer (the seasons with moderate to large sample sizes) were similar to those of Yates (1978).

The greatest numbers of ovigerous *S. erythrodactyla* were found in summer (Table 4.7C), which is similar to the pattern described by Yates (1978), but the proportion of ovigerous females in each zone at Patonga was much greater than that in the present study. Collections from Gymea Bay also indicated greatest prevalence of ovigerous females in summer and none in winter, with smaller numbers in spring and early autumn (Green and Anderson 1973).

Very little work has been done on the biology and life histories of *H. cordiformis*, *P. laevis* and *S. erythrodactyla*. Griffin (1971), Yates (1978) and the present study provide information on size-frequencies, sex ratios and temporal aspects of ovigery. In addition, Yates (1978) examined seasonal changes in gonads and oogenesis in these species, and Green and Anderson (1973) described the first zoeal stage of the two grapsid species. The seasonality of recruitment, growth, longevity and mortality have not yet been examined, although this information is important. Such information may provide explanations for the great variability in patterns among swamps, zones and other spatial and temporal scales in the present and other studies.

CHAPTER 5. MECHANISMS UNDERLYING DISTRIBUTIONAL PATTERNS BETWEEN MICROHABITATS (MOUNDS VS. FLATS)

Introduction

H. cordiformis were most abundant in mounds, P. laevis were most abundant in flats and S. erythrodactyla were distributed in similar abundances between these two microhabitats (Chapter 3). The two most likely mechanisms underlying the different distributional patterns are habitat selection (preference) and interspecific interactions. Of the many factors which have been investigated to explain distributional patterns of intertidal organisms (e.g recruitment, disturbance, physiological tolerance, etc.; see reviews by Connell 1975; Sousa 1985; Underwood 1979; Underwood and Denley 1984), only preference and interspecific interactions (e.g. predation, displacement or facilitation) are relevant to the small spatial separation between mounds and flats. Crabs readily traverse both microhabitats, and all three species have been found in burrows in each microhabitat.

The model of habitat selection proposes that H. cordiformis were more abundant in mounds and P. laevis more abundant in flats because they chose (preferred) to build and/or occupy burrows in mounds and flats, respectively. S. erythrodactyla, however, were distributed more evenly between these microhabitats because they demonstrated no preference for either.

Although many studies of intertidal distributions of burrowing crabs have inferred that preference explains the observed distributional patterns (primarily zonation), the majority of these have not actually tested this hypothesis (e.g. Allen and Curran 1974; Jones and Simons 1982; Ono 1959;

Snelling 1959; and many others). Some authors have examined preferences by laboratory experiments (Ringold 1979 and Teal 1958 for fiddler crabs; Warburg and Shuchman 1979 for sand crabs, genus Ocypode; and Griffin 1971 and Yates 1978 for various grapsids and ocypodids, including those of the present study). These authors have extrapolated results from laboratory experiments to natural populations.

Bertness and Miller (1984) examined burrowing ability and preference of the mud fiddler crab Uca pugnax in experiments in a variety of substrata in the field. Density of roots of cordgrass, sediment stability, presence of supporting structures (e.g. emergent vegetation), hardness of the substratum and zonal origin of sediments (i.e. substratum from the seaward zone, mid-marsh zone and upper zone) all proved important determinants of the observed zonal distribution of crabs and their burrows.

To test the importance of preference as a mechanism underlying the observed distributions of crabs in the present study, each species was added alone (at natural density) to enclosures containing a mound to one side and a flat to the other. Preference was demonstrated by the occurrence of significantly more crabs and/or their burrows in one microhabitat.

To examine the effect of crowding on preference, other enclosures were used with experimentally increased densities. These experiments determined whether crabs, when crowded, retained an absolute preference for one microhabitat or whether some crabs would be displaced into the less-preferred microhabitat and forced to make burrows there.

The effect of crowding on the ratio of burrows to crabs (per enclosure) was also examined. An earlier study by McKillup and Butler (1979) demonstrated that *Helograpsus haswellianus* (another burrowing mangrove crab) ceased digging new burrows before the substratum became weak enough to collapse. The maximum density of burrows in a volume of substratum before collapse was determined by addition of artificial burrows. In nature, most burrows of *H. haswellianus* (and the species in the present study) contain a single crab. Under experimentally crowded conditions, however, two or more *H. haswellianus* occupied existing burrows once the maximum density of burrows (before collapse) had been reached. The possibility that *H. cordiformis* demonstrates a similar behaviour was therefore examined. A similar study was irrelevant for the other two species, because they make few proper burrows and instead make shallow depressions.

Ancillary experiments were done to identify characteristics of the microhabitats that might enhance preference. Availability of unoccupied burrows was one factor tested. During the 3.5 years of the present study, crabs were never observed to create new burrows except in enclosures devoid of burrows. Instead, crabs wandering over the surface challenged burrow-owners for their residence or explored open burrows until an unoccupied one was found. The presence of unoccupied burrows in mounds or flats might, therefore, enhance the attractiveness of the microhabitat. To test this, two types of experiments were done. First, artificial 'burrows' were provided only in the less-preferred microhabitat in an enclosure. If availability of burrows enhanced preference, a significantly greater proportion of crabs would be found in that microhabitat than in enclosures without such 'burrows.'

In the second experiment natural densities of 'burrows' were added to each microhabitat to determine any effects on the choice of microhabitat. Further experiments were designed to examine which features of mounds were important in habitat selection. Crabs might respond to the topography (better drainage, slightly longer period of emersion, etc.) or to the composition (size of sediments, organic content, etc.) of mounds or flats. Experimental enclosures with natural mounds and flats or mounds and flats made from the opposite type of material (e.g. mounds of sediments from naturally flat areas) were used to distiguish these criteria.

Additional experiments were used to determine the potential influences of other species of crabs on the microhabitat preferences of H. cordiformis, P. laevis and S. erythrodactyla. The only experimental investigation of the effects of interspecific interactions on distributions of crabs was Teal (1958) who tested preferences of three species of fiddler crabs for mud versus sand and submerged versus emersed substratum. Teal (1958) concluded that certain combinations of species and types of substratum resulted in displacement of crabs from their preferred microhabitat. It was, however, unclear how he was able to identify which species made which burrows and, thus, discriminate between the responses of each species. The design of his experiment was also faulty in that treatments were not replicated. The effects of sequential additions were not examined although the resulting distributional patterns might have differed from those seen when species were added simultaneously: the first species added might have had an advantage, and a species added later might have been displaced into a less-preferred habitat.

Methods and materials

Habitat selection (Preference)

1. Preference for natural mounds and flats, and effects of crowding

To provide crabs with a choice between mounds and flats, 0.40-0.45 m^2 sites containing both types of microhabitat were enclosed by formica barriers (see Chapter 2 for details). Arenas had a mound to one side of the enclosed area and a flat of approximately equal area to the other side. To test the accuracy of estimating equal proportions of mound and flat for each enclosure, proportions of these areas represented by mounds were calculated for the 9 enclosures of the first preference experiment. The mean proportion of mound per enclosure was not significantly different from 0.50 (t-test, $P > 0.50$). Original occupants of burrows in enclosures were removed over several days, and each burrow was plugged with sediment adjacent to the entrance. All of the experiments described in this chapter were done in the midmangrove zone.

The experiment with *H. cordiformis* was done at Careel Bay (16-30 December 1983), *P. laevis* at Woolooware Bay West (10-18 November 1985) and *S. erythrodactyla* at Woolooware Bay West (2-9 December 1985).

To facilitate censusing of crabs and their burrows, only medium- to large-sized individuals were used. (The minimum carapace lengths were 10 mm, 15 mm and 15 mm for *H. cordiformis* , P. *laevis* and *S. erythrodactyla*, respectively.) Except for experiments on crowding, natural densities of 20 *H. cordiformis*, 4 *P. laevis* and 4 *S. erythrodactyla* per enclosure were used. Dead crabs were replaced at each census to maintain initial densities.

Every 2-3 days, the numbers of crabs emerging from burrows in each microhabitat were recorded during a 10-minute period after emergence of the first crab. Numbers of open burrows in each microhabitat were also noted. Those of *H. cordiformis* were easily distinguished from those of the grapsids (see Chapter 2). *P. laevis* and *S. erythrodactyla* made few 'proper' burrows (i.e. burrows descending below the surface). Instead, they tended to create shallow depressions in the surface of the substratum. In many censuses all of the enclosed grapsids were on the surface of the substratum or in these depressions, and in these cases the censuses did not require the 10-minute period of observation. Analyses of locations of burrows for *P. laevis* and *S. erythrodactyla* included depressions. Both species readily occupied artificial 'burrows', and the entrances to these attained the characteristic shape for these species after a few days of occupation.

Except for the first preference experiment with *H. cordiformis*, locations of crabs were determined on the basis of where crabs emerged from burrows, where they occupied depressions or where they were on the surface at the start of the period of observation. The exception noted above involved recording locations of *H. cordiformis* at the end of the census of each enclosure, by which time many crabs had moved between microhabitats.

Counts of crabs and burrows provided two different measurements of preference. The first indicated where crabs chose to occupy burrows (or depressions) and the second measurement indicated where crabs chose to create these structures. This latter measurement was considered to be a stronger indicator of preference because of the investment of energy required to make burrows (especially) and depressions, and because distributions of these structures were more permanent than distributions of crabs, which readily travsersed both microhabitats.

Experiments testing the preference of crabs between mounds and flats incorporated treatments with natural densities and 2.5x and 5x natural densities. To test for the possibility that crabs aggregated and/or contructed burrows in clusters, regardless of microhabitat, controls of all-mound and all-flat enclosures were used. For censusing, these enclosures were divided in two by a line drawn on the substratum. The intermediate density (of 2.5x natural) was used in the controls. Three replicate enclosures were used for each of the five treatments above.

2. Effects of availability of unoccupied burrows on preference

To test if the availability of unoccupied burrows would enhance preference for a microhabitat, half-mound/half-flat enclosures were erected (as before), but artificial burrows (='burrows') were made in one or both microhabitats. To simulate natural burrows, 'burrows' descended at a slight angle from the vertical, were 25-30 mm in diameter and approximately 30 cm deep. Use of a tyre iron (with one flat, angled end) allowed creation of a somewhat enlarged terminal chamber (again, simulating natural burrows). 'Burrows' were added on the same day as crabs, because unoccupied 'burrows' begin to collapse 3-5 days after creation. A toothpick was placed adjacent to the entrance of each 'burrow' to allow discrimination between these and burrows made by crabs.

Two series of experiments were done with 'burrows' at Woolooware Bay East from March to May 1986. In the first series, 'burrows' were provided in only the less-preferred microhabitat (as determined from the previous experiment). Enclosures without 'burrows' served as controls and provided a second trial of the preference experiment for natural mounds and flats in the absence of burrows. Three replicate enclosures were used for each of the two treatments.

In the second series, 'burrows' were provided in natural densities in each microhabitat: 13 in mounds and 5 in flats. These means were determined from counts of 10 quadrats in each natural microhabitat. Six replicate enclosures were used for each species.

3. Roles of topography and material in habitat selection

Two characteristics of mounds and flats were examined for their effects on habitat selection by _H. cordiformis_ and _P. laevis_. Three replicate enclosures were used for each of nine treatments in which topography and material were manipulated:

TREATMENTS

('Natural' = Undisturbed)

1. Natural mound vs. natural flat
2. Natural flat vs. natural flat
3. Natural mound vs. natural mound
4. Flat of mound material (disturbed) vs. natural flat
5. Flat of flat material (disturbed) vs. natural flat
6. Mound of flat material (disturbed) vs. natural flat
7. Mound of mound material (disturbed) vs. natural flat
8. Natural mound vs. mound of flat material (disturbed)
9. Natural mound vs. mound of mound material (disturbed)

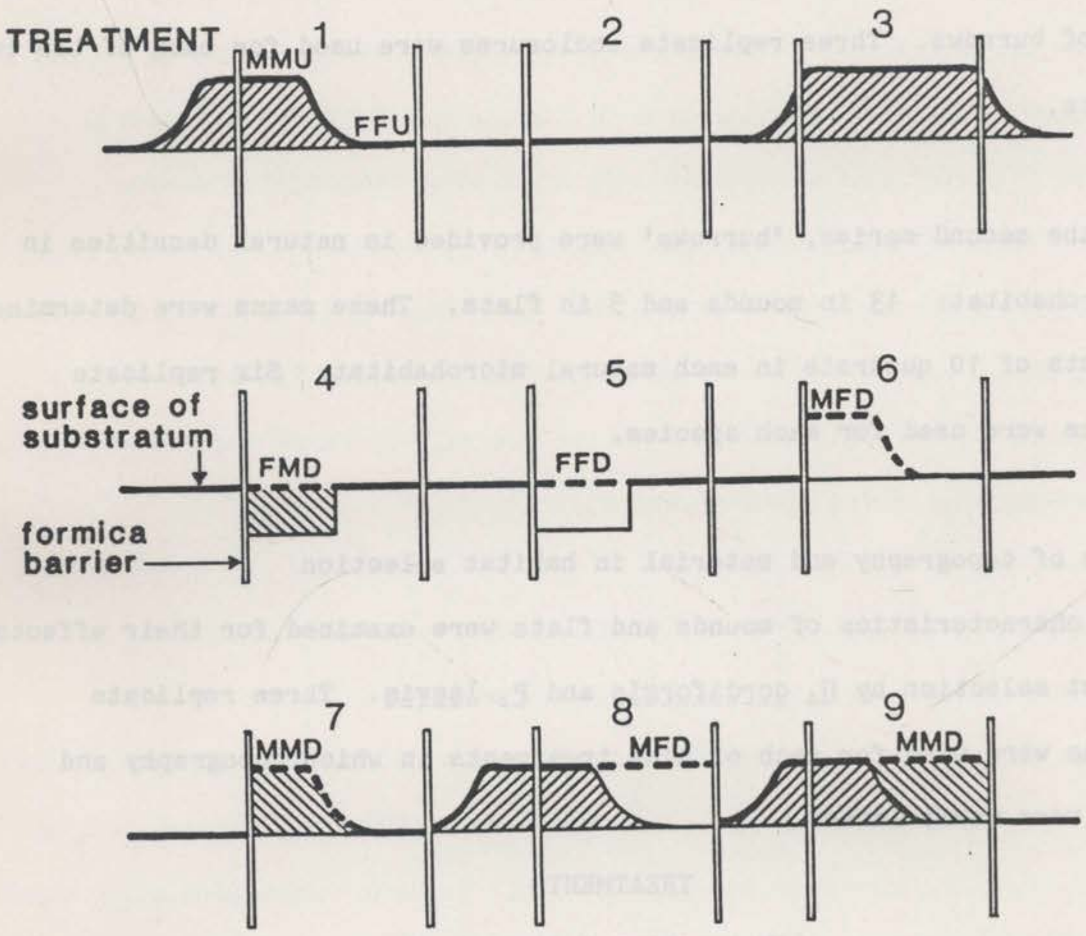

Figure 5.1. Diagram of 9 treatments used to examine the role of topography and material of the substratum in habitat selection. ▨ = material from mound; ▧ = disturbed material from mound; ☐ = material from flat. —— = undisturbed surface; - - - - = disturbed surface. Three-letter codes indicate (in order) topography (Mound or Flat), origin of material (Mound or Flat), and whether Disturbed or Undisturbed.

These treatments are illustrated in Figure 5.1. Disturbance represented substratum that was removed and transplanted. An attempt was made to retain the integrity of the sediments (i.e. consolidation by peg roots and nutritive roots). As in other experiments, original occupants of burrows were removed and their burrows filled in with substratum adjacent to the entrance. All treatments except Treatments 2 and 3 were run at Careel Bay (from 19-30 May 1984 for *H. cordiformis* and from 13-27 June 1984 for *P. laevis*). Treatments 2 and 3 were the all-flat and all-mound controls, respectively, from the preference and crowding experiment for *H. cordiformis* (16-30 Dec. 1983, Careel Bay) and *P. laevis* (10-18 Nov. 1985, Woolooware Bay West). These two treatments could not be run concurrently with the other seven treatments because of the limited time available to census crabs during diurnal periods of emersion.

Interspecific interactions

At Woolooware Bay East, simultaneous and sequential additions of a second species of crab (to enclosures) were used to examine interspecific interactions. For experiments with sequential additions, natural densities of each species were added to half-mound/half-flat enclosures and allowed to 'settle' for 7 days. During this time, censuses of crabs and burrows every 2-3 days were made to record distributions before addition of the second species. (These data, incidentally, represented a third trial of the single species preference experiments.) On Day 7, the second species was added to enclosues. Subsequent censuses during the next week recorded the positions of each species and its burrows. Because burrows and depressions made by or occupied by *P. laevis* and *S. erythrodactyla* are indistinguishable, analyses of burrows were not done for treatments with this combination of species.

Table 5.1. Numbers of crabs and burrows in enclosed mounds and flats in 2-3 trials of preference experiments with single species at natural densities. Locations of crabs were recorded as they emerged onto the surface. Locations of *H. cordiformis* in Dec. 1983 were noted at the end of the 10-minute period of observation and were not included in the analysis. Burrows for *P. laevis* and *S. erythrodactyla* were mostly counts of depressions (see text). In Dec. 1985, too few depressions were made by *S. erythrodactyla* to include in the analysis. Numbers of crabs and burrows have been pooled from 3 or 6 enclosures [*n*] per trial.

		H. CORDIFORMIS			*P. LAEVIS*			*S. ERYTHRODACTYLA*		
DATES OF TRIALS:		DEC 83	MAR-APR 86	APR 86	NOV 85	APR 86	APR 86	DEC 85	APR 86	MAY 86
(CENSUS):		(DAY 5)	(DAY 6)	(DAY 7)	(DAY 8)	(DAY 7)	(DAY 7)	(DAY 7)	(DAY 7)	(DAY 7)
[*n*]:		[3]	[3]	[3]	[3]	[3]	[6]	[3]	[6]	[3]
CRABS	MOUND	-	43	34	1	8	8	6	11	5
	FLAT	-	7	11	11	3	15	5	10	7
	χ^2		1.68 (1 df)			10.31 (2 df)			0.47 (2 df)	
	P		> 0.10			= 0.005			> 0.50	
BURROWS	MOUND	74	60	50	4	7	13	-	12	5
	FLAT	37	11	11	17	5	16	-	9	7
	χ^2		9.23 (2 df)			5.83 (2 df)			0.01 (1 df)	
	P		< 0.01			> 0.05			> 0.50	

Because distributional data for each species after addition of the second species were not independent of data prior to addition, analyses of interspecific effects compared final distributions to those recorded in the second single species preference experiments (which were also done at Woolooware Bay East as controls for treatments with artificial 'burrows' in one microhabitat only).

Three replicate enclosures were used for each of two treatments for each pair of species (Sp. X then Sp. Y, and Sp. Y then Sp. X), for a total of 18 enclosures. This experiment was done from 4-17 April 1986, and data for analyses were from Day 6 (after addition of the second species).

The experiment with simultaneous additions of a second species involved only three treatments (one for each pair of species) but was otherwise identical in design to the previous experiment. The experiment was done from 4-18 May 1986, and data for analyses were from Day 7.

Results

Habitat selection by single species

1. H. cordiformis

a. Mounds versus flats

H. cordiformis clearly preferred mounds to flats (Table 5.1). Among the three trials of this experiment, the magnitude of the difference in numbers of crabs and burrows was variable, ranging from 2-6 times greater abundance in mounds. Although crabs primarily chose to burrow and inhabit burrows in mounds, H. cordiformis readily moved between mounds and flats during their period of activity on the surface.

Table 5.2. Mean proportion (+ S.E.) of crabs and their burrows in the mound half of experimental enclosures or from a randomly chosen half of all-mound or all-flat controls on the final day of censusing (Day 14 for *H. cordiformis* and Day 8 for *P. laevis*). Data for each analysis of variance were untransformed, and Cochran's test was not significant, *P* > 0.05. Treatments 1x, 2.5x and 5x used natural densities (x) and multiples of these values: (x) = 20 H. *cordiformis* and 4 *P. laevis*. MC = all-mound control and FC = all-flat control. *n* = 3 enclosures.

	TREATMENTS						
SPECIES	1X	2.5X	5X	MC	FC	*P*-VALUE FROM ANOVA	SNK TESTS (*P* = 0.05)
H. cordiformis							
CRABS:	0.60	0.64	0.65	0.57	0.37	> 0.10	None
	(0.08)	(0.01)	(0.11)	(0)	(0.02)		
BURROWS:	0.75	0.93	0.76	0.49	0.49	< 0.001	FC=MC<1x=5x<2.5x
	(0.04)	(0.01)	(0.08)	(0.03)	(0.03)		
P. laevis							
CRABS:	0.11	0.20	0.36	0.16	0.61	> 0.05	None
	(0.01)	(0.12)	(0.08)	(0.08)	(0.15)		
DEPRESSIONS:	0.20	0.42	0.52	0.56	0.47	< 0.05	1X=2.5x=5x=MC=FC
	(0.04)	(0.04)	(0.07)	(0.11)	(0.02)		

Crowding did not cause a significant number of H. cordiformis to be displaced from their preferred microhabitat: at 2.5x and 5x natural density, more crabs continued to make burrows in mounds than in flats (Chi-squared goodness-of-fit tests on pooled numbers from enclosures for each density, $P < 0.005$; analysis of variance, Table 5.2). Similar analyses indicated no significant difference between microhabitats at natural density, but a greater proportion of crabs on mounds than flats at 2.5x and 5x natural density (Chi-squared tests, $P < 0.005$). Analyses of variance indicated no significant differences amongst the three density treatments and the all-mound and all-flat controls (Table 5.2). The somewhat smaller proportion of crabs in one random half of the all-flat controls suggests merely that at any given time, crabs might have 'crowded' into one portion of an enclosure.

These patterns of distribution of H. cordiformis (based on data from Day 14) had been established by Day 3 or Day 5 (Figure 5.2). Plots of 5x density resembled those of the controls. Similar experiments would, therefore, require approximately one week for final, stable patterns to emerge; for this reason, subsequent experiments were usually run for 6-8 days.

At natural density, the number of open burrows per enclosure was almost twice that of the number of crabs emerging (Table 5.3). This ratio was significantly greater than that at 2.5x natural density in the half-mound/half-flat enclosures and all-mound controls (approximately 1:1) and at 5x natural density and 2.5x natural density in the all-flat controls (0.70:1).

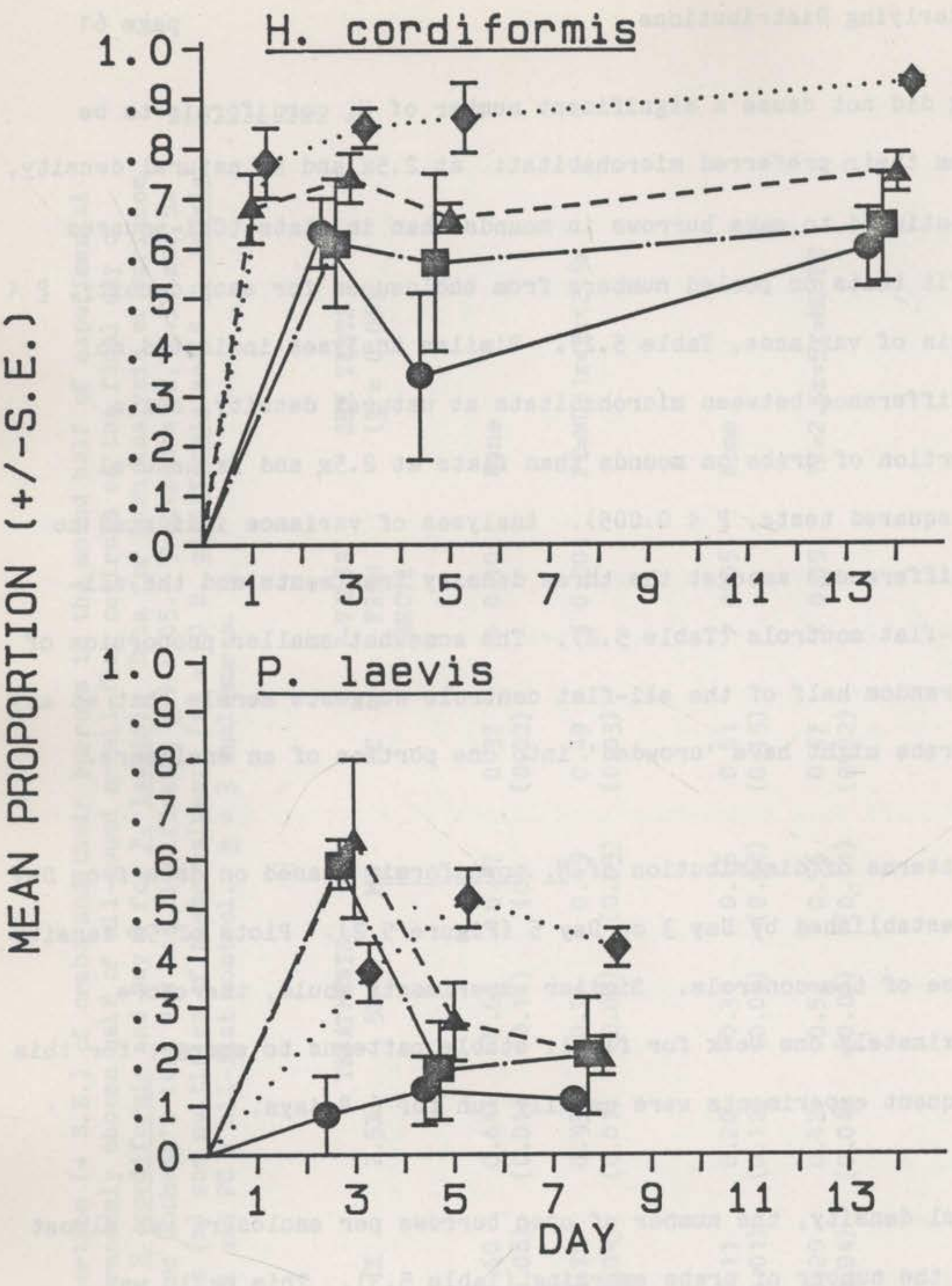

Figure 5.2. Mean proportion of crabs and burrows (+ S.E.) in the mound half of enclosures containing crabs at 1x and 2.5x natural density. Plots of 5x natural density and controls were similar and have been omitted for simplicity. Circles = crabs, natural density; triangles = burrows, natural density; squares = crabs, 2.5x natural density; and diamonds = burrows, 2.5x natural density. _n_ = 3 enclosures.

Table 5.3. Mean ratio of the number of burrows to the number of emerging crabs (+ S.E.) in enclosures with 1x, 2.5x and 5x the natural density of crabs. Abbreviations for treatments are as in Table 5.2. For *P. laevis*, counts of burrows included counts of depressions. Data are untransformed; *n* = 3 enclosures.

SPECIES (& CENSUS)	TREATMENTS					*P*-VALUE FROM ANOVA	SNK TESTS (*P* = 0.05)
	1X	2.5X	5X	MC	FC		
H. cordiformis (Day 5)	1.84	0.97	0.75	1.20	0.69	< 0.001	2.5x=5x=MC=FC<1x
	(0.27)	(0.08)	(0.04)	(0.06)	(0.01)		
P. laevis (Day 8)	1.73	2.34	1.28	1.75	1.15	< 0.05	1x=2.5x=5x=MC=FC
	(0.27)	(0.36)	(0.11)	(0.26)	(0.08)		

Table 5.4. Numbers of crabs and new burrows in enclosed mounds and flats, with and without artificial 'burrows'. Counts of new burrows for *P. laevis* and *S. erythrodactyla* included depressions made by these species (as in Table 5.1). Data have been pooled from 3 enclosures (for the trials without 'burrows' or with 'burrows' in one half only) and from 6 enclosures (for the trials with 'burrows' in each half). For the treatment with 'burrows' in each half, natural densities of 13 in the mound half and 5 in the flat half were added. Natural densities of 20 *H. cordiformis*, 4 *P. laevis* and 4 *S. erythrodactyla* were used. These experiments were done from March to May 1986; data are from Day 6 or Day 7 (the final census for each trial). For *S. erythrodactyla* too few depressions were made in the treatment with 'burrows' in each half to include these data in the analysis.

	H. CORDIFORMIS			*P. LAEVIS*			*S. ERYTHRODACTYLA*		
NO. OF BURROWS ADDED:	NONE	20 IN FLAT HALF ONLY	NAT. DENS. IN EACH HALF	NONE	4 IN MOUND HALF ONLY	NAT. DENS. IN EACH HALF	NONE	4 IN FLAT HALF ONLY	NAT. DENS. IN EACH HALF
CRABS- MOUND	43	34	80	8	9	16	5	4	17
FLAT	7	19	25	3	2	7	7	8	6
χ^2		6.70 (2 df)			0.57 (2 df)			6.47 (2 df)	
P		< 0.05			> 0.50			< 0.05	
BURROWS- MOUND	60	41	31	7	1	1	5	4	-
FLAT	11	2	0	5	2	5	4	1	-
χ^2		7.60 (2 df)			2.94 (2 df)			0.84 (1 df)	
P		< 0.025			> 0.10			> 0.25	

b. Artificial burrows

The presence of artificially created 'burrows' in the flat half or in both halves of enclosures did not affect the nature of the preference of H. cordiformis for mounds (Table 5.4), but did increase the proportions of crabs occupying burrows in the flats relative to crabs digging and occupying burrows in this microhabitat when no 'burrows' were provided. When natural densities of 'burrows' were provided in mounds and flats, numbers of crabs in each microhabitat did not differ significantly from expected frequencies derived from the numbers of 'burrows' provided in mounds and flats (Chi-squared goodness-of-fit test, $P > 0.25$). Crabs made fewer new burrows in flats already provided with 'burrows' than in flats initially devoid of burrows. These results suggest that providing burrows in flats made this microhabitat more desirable than it would have been otherwise.

c. Topography and material

Both topography per se and composition of mounds or flats influenced the habitat selection of H. cordiformis. Crabs did not, for example, prefer mounds over undisturbed flats when the mound was made from sediments from the surface of flats (= 'flat material'; Table 5.5 and Appendix 5.1). Part of this decreased preference was clearly a response to disturbance of the substratum: significantly fewer crabs occupied burrows in mounds of disturbed mound material than in undisturbed (natural) mounds. The importance of the role of material was, however, indicated by significantly fewer crabs in mounds of disturbed flat material than in mounds of disturbed mound material.

Table 5.5. Mean proportion of *H. cordiformis* and their burrows (+ S.E.) in the mound half of enclosures on Day 11 of the experiments on topography and composition of substrata (= material) (May 1984). Three-letter codes and numbers in brackets, [ ], refer to the treatment associated with each mean, as per Figure 5.1. n = 3 enclosures. Data are untransformed and from the type of mound described in the columns of the table. Analyses of variance of these data are in Appendix 5.1.

	COMPOSITION OF MOUND HALF (= F1)			
CONTRASTED WITH (= F2)	MOUND MATERIAL, UNDISTURBED (MMU)	MOUND MATERIAL, DISTURBED (MMD)	FLAT MATERIAL, DISTURBED (MFD)	SNK TESTS ON F1 (P = 0.05)
Crabs:				
Mound, undisturbed (MMU)	0.57 (0.003) [3]	0.33 (0.11) [9]	0.12 (0.07) [8]	MMU > MMD > MFD
Flat, undisturbed (FFU)	0.93 (0.04) [1]	0.52 (0.02) [7]	0.28 (0.07) [6]	
Burrows:				
Mound, undisturbed (MMU)	0.49 (0.03) [3]	0.41 (0.06) [9]	0.30 (0.03) [8]	MMU > MMD > MFD
Flat, undisturbed (FFU)	0.73 (0.02) [1]	0.56 (0.04) [7]	0.48 (0.07) [6]	

Comparison of overall means of F2 (= columns pooled for each row):

	PROP'N. IN MOUND VS. UNDISTURBED MOUND		PROP'N. IN MOUND VS. UNDISTURBED FLAT	
Crabs:	0.34	<	0.58	(P < 0.001, ANOVA)
Burrows:	0.40	<	0.59	(P < 0.005, ANOVA)

There were similar effects of topography, material and disturbance on locations of burrows (Table 5.5). The differences among the proportions of burrows in the three kinds of mounds were, however, not as great as the differences in numbers of crabs. When contrasted with undisturbed flats, for example, the difference in the proportions of burrows in natural mounds versus mounds of flat material was 0.25 whereas the corresponding difference in proportions of crabs was 0.65.

In summary, regardless of the nature of the second half of enclosures, H. cordiformis clearly preferred the material of undisturbed mounds to that of disturbed mounds, and this latter material to that of disturbed flats. More crabs chose to occupy burrows in mounds when these were adjacent to flats than when these were adjacent to other kinds of mounds. (Note that the lack of significant interaction between these two factors in the anlyses of variance validated the 'pooling' of results associated with the above summary; Appendix 5.1.)

A similar set of analyses, but this time comparing the proportions of H. cordiformis in undisturbed flats to three kinds of mounds and three kinds of flats, again indicated that both topography and material were important in habitat selection. In these analyses, however, there was a significant interaction between both factors with respect to locations of crabs (Table 5.6; Appendix 5.2). Fewer crabs occupied burrows in undisturbed flats when these were adjacent to undisturbed mounds than when undisturbed flats were adjacent to disturbed mounds (of mound material). Fewer crabs were found in undisturbed flats adjacent to mounds of disturbed mound material than in undisturbed flats adjacent to mounds of disturbed flat material. The

Table 5.6. Mean proportion of *H. cordiformis* and their burrows (+ S.E.) in the undisturbed flat half of enclosures on Day 11 of the experiment on topography and substratum (= material)(May 1984). Three-letter codes and numbers in brackets, [ ], refer to the treatment associated with each mean, as per Figure 5.1. $n = 3$ enclosures. ∨ , ∧ and ‖ in table indicate results from SNK tests ($P = 0.05$). (ANOVA of burrows indicated proportions did not differ significantly, $P > 0.05$). Data are untransformed. Analyses of variance of these data are in Appendix 5.2. SNK tests for F1 compare mean proportions in undisturbed flats when these were opposite mounds and other flats. (For example, 'opp. MMU' indicates the mean proportion in the undisturbed flat half when this was *opposite* a *m*ound of *m*ound material, *u*ndisturbed.)

	COMPOSITION OF HALF OPPOSITE UNDISTURBED FLAT (= F1)			
CONTRASTED WITH (= F2)	CORRECT MATERIAL FOR GIVEN TOPOGR., UNDISTURBED (MMU OR FFU)	CORRECT MATERIAL FOR GIVEN TOPOGR., DISTURBED (MMD OR FFD)	WRONG MATERIAL FOR GIVEN TOPOGR., DISTURBED (MFD OR FMD)	SNK TESTS ON F1 ($P = 0.05$)
Crabs:				
Mound	0.07 (0.04) [1]	0.48 (0.02) [7]	0.72 (0.07) [6]	opp. MMU < opp. MMD < opp. MFD
	∧	‖	∨	
Flat	0.37 (0.02) [2]	0.59 (0.05) [5]	0.27 (0.09) [4]	opp. MMU = opp. MMD < opp. MFD
Burrows:				
Mound	0.27 (0.02) [1]	0.44 (0.04) [7]	0.52 (0.07) [6]	None ($P > 0.05$, ANOVA)
Flat	0.49 (0.03) [2]	0.56 (0.10) [5]	0.47 (0.03) [4]	

preference of *H. cordiformis* for flats, therefore, increased with increasing 'abnormality' of the mounds adjacent to these flats. Such a hierarchic response was not observed when undisturbed flats were contrasted with flats of varying degrees of 'abnormality.' This might have contributed to the significant interaction between factors indicated by the analysis of variance (Appendix 5.2).

Crabs did not demonstrate any preference between undisturbed flats and flats of disturbed flat material, but appeared to prefer flats of disturbed mound material over undisturbed flats (but this was not significant in an SNK test). When undisturbed flats were adjacent to mounds made from disturbed mound material or adjacent to flats of disturbed flat material, *H. cordiformis* demonstrated no significant preference. Finally, when crabs were presented with a choice between undisturbed flats and mounds of disturbed flat material or flats of disturbed mound material, they preferred flats of mound material.

2. *P. laevis*

a. Mounds versus flats

At natural density, *P. laevis* tended to prefer flats, although results of experiments were much more variable for this species than for *H. cordiformis*. Proportions of crabs in each microhabitat varied significantly among three separate trials of the preference experiment (Table 5.1). Overall, proportions of burrows and depressions made by *P. laevis* did not differ significantly between mounds and flats, but significantly more burrows and depressions were made in flats in the first preference experiment in

November 1985. Like H. cordiformis, unenclosed P. laevis moved freely between microhabitats.

At natural density and at 2.5x and 5x natural density, the proportions of P. laevis in flats were significantly greater than in mounds, and these proportions did not differ significantly (Table 5.2). Crowding, therefore, did not cause crabs to be displaced from their preferred microhabitat in flats. The distribution of depressions made by this species was, however, affected by crowding: a greater proportion of depressions were made in mounds when P. laevis were enclosed at 2.5x and 5x natural density. Thus, some P. laevis were displaced from their preferred microhabitat, at least with respect to selection of a place in which to burrow. At 2.5x and 5x natural density, similar numbers of depressions were made in mounds and flats. Results from controls did not differ from expectations: depressions were fairly evenly distributed over the enclosed substrata.

The numbers of depressions made by P. laevis were greater than or equal to the numbers of emerging crabs (Table 5.3). Because most of these data represent shallow depressions in the surface rather than deep burrows, it is not surprising that the ratios (of depressions to crabs) at each density were generally greater than those for H. cordiformis which dig deep burrows. Much less time and energy are required to create a depression than to construct a proper burrow.

The variability among censuses of the distribution of P. laevis and their burrows between microhabitats was greater than that seen for H. cordiformis (Figure 5.2). Plots of 5x and controls resembled patterns observed for crabs and burrows at natural and 2.5x natural density and were omitted (for simplicity) from Figure 5.2. A more or less stable pattern was established by Day 5 or day 7 of the experiment. Subsequent experiments of similar design were run for approximately one week.

b. Artificial burrows

P. laevis were more abundant in mounds than flats when 'burrows' were provided in mounds only (Table 5.4). This result might reflect that these crabs will occupy pre-existing burrows (because they cannot construct their own) and were more abundant in mounds because 'burrows' were available in only that microhabitat. Crabs were also more abundant in mounds when 'burrows' were added to mounds and flats, perhaps because 3x more 'burrows' were in mounds than flats. Although these two results might reflect attraction to available burrows, *P. laevis* was occasionally more abundant in mounds even in the absence of 'burrows' (see Table 5.1). Other evidence that providing burrows does affect *P. laevis* is that numbers of crabs in each microhabitat were not significantly different from those expected from the distribution of artificial 'burrows' (Chi-squared goodness-of-fit test, $P >$ 0.50).

The provision of 'burrows' in mounds or in mounds and flats did not significantly alter the distribution of new burrows and depressions between microhabitats (Table 5.4). The numbers of new burrows and depressions were, however, very small.

Table 5.7. Mean proportion of *P. laevis* and their depressions (+ S.E.) in the mound half of enclosures on Day 12 of the experiment on topography and substratum (= material)(June 1984). Three-letter codes and numbers in brackets, [ ], refer to the treatment associated with each mean, as per Figure 5.1. *n* = 3 enclosures. Data are untransformed and from the type of mound described in the columns of the table. Analyses of variance of these data are in Appendix 5.2.

	COMPOSITION OF MOUND HALF (= F1)			
CONTRASTED WITH (= F2)	MOUND MATERIAL, UNDISTURBED (MMU)	MOUND MATERIAL, DISTURBED (MMD)	FLAT MATERIAL, DISTURBED (MFD)	SNK TESTS ON F1 (*P* = 0.05)
Crabs:				
Mound, undisturbed (MMU)	0.16 (0.09) [3]	0.52 (0.24) [9]	0.51 (0.25) [8]	None (*P* > 0.25, ANOVA)
Flat, undisturbed (FFU)	0.33 (0.17) [1]	0.83 (0.17) [7]	0.68 (0.09) [6]	
Depressions:				
Mound, undisturbed (MMU)	0.56 (0.11) [3]	0.48 (0.03) [9]	0.43 (0.07) [8]	None (*P* > 0.25, ANOVA)
Flat, undisturbed (FFU)	0.49 (0.10) [1]	0.77 (0.05) [7]	0.71 (0.06) [6]	

Comparison of overall means of F2 (= columns pooled for each row):

	PROP'N. IN MOUND VS. UNDISTURBED MOUND		PROP'N. IN MOUND VS. UNDISTURBED FLAT	
Crabs:	0.40	=	0.61	(*P* > 0.10, ANOVA)
Burrows:	0.49	<	0.66	(*P* < 0.05, ANOVA)

c. Topography and material

Examination of the importance of topography and material in preference indicated that the proportions of crabs in the mound half of enclosures were influenced by neither of these factors (Tables 5.7 and 5.8; Appendices 5.1 and 5.2). When presented with a choice between undisturbed flats and mounds or other kinds of flats, P. laevis made significantly more depressions in mounds of disturbed mound material or disturbed flat material than in undisturbed mounds (Table 5.8; small proportions in table mean large proportions in mounds). Also, crabs made more depressions in mounds of disturbed mound material than in flats of disturbed flat material; no other differences were significant.

In summary, the effects of topography and material on habitat selection were significant with respect to locations of depressions but not to location of crabs between mounds and flats. Although topography, material and disturbance were all shown to influence the distribution of depressions, the nature of these effects was inconsistent; therefore, the role of these factors in the tendency of P. laevis to occupy burrows in or make depressions in flats remains unclear.

3. S. erythrodactyla

a. Mounds versus flats

When enclosed at natural density in the absence of other species, S. erythrodactyla and their depressions were distributed in similar proportions between mounds and flats (Table 5.1). This pattern reiterated the distribution of this species determined by earlier sampling with traps and

Table 5.8. Mean proportion of *P. laevis* and their depressions (+ S.E.) in the undisturbed flat half of enclosures on Day 12 of the experiment on topography and composition of substratum (= material)(June 1984). Three-letter codes and numbers in brackets, [ ], refer to the treatment associated with each mean, as per Figure 5.1. *n* = 3 enclosures. ∧ , ∨ and || in table indicate results from SNK tests ($P = 0.05$). (ANOVA of burrows indicated proportions did not differ significantly, $P > 0.05$). Data are untransformed. Analyses of variance of these data are in Appendix 5.2. SNK tests for F1 compare mean proportions in undisturbed flats when these were opposite mounds and other flats. (For example, 'opp. MMU' indicates the mean proportion in the undisturbed flat half when this was *opposite* a mound of mound material, undisturbed.)

	COMPOSITION OF HALF OPPOSITE UNDISTURBED FLAT (= F1)			
CONTRASTED WITH (= F2)	CORRECT MATERIAL FOR GIVEN TOPOGR., UNDISTURBED (MMU OR FFU)	CORRECT MATERIAL FOR GIVEN TOPOGR., DISTURBED (MMD OR FFD)	WRONG MATERIAL FOR GIVEN TOPOGR., DISTURBED (MFD OR FMD)	SNK TESTS ON F1 ($P = 0.05$)
Crabs:				
Mound	0.67 (0.17) [1]	0.17 (0.17) [7]	0.32 (0.09) [6]	None ($P > 0.10$, ANOVA)
Flat	0.61 (0.15) [2]	0.54 (0.14) [5]	0.36 (0.19) [4]	
Depressions:				
Mound	0.51 (0.10) [1]	0.23 (0.05) [7]	0.29 (0.06) [6]	opp. MMU > opp. MMD = opp. MFD
	||	∧	||	
Flat	0.47 (0.02) [2]	0.57 (0.04) [5]	0.46 (0.06) [4]	opp. FFU = opp. FFD = opp. FMD

quadrats (Chapter 3). The lack of preference for either microhabitat can, therefore, explain the distributional pattern of the population at large.

Because S. erythrodactyla demonstrated no clear preference for mounds or flats, no experiment was done testing the effects of crowding (as done for the other two species).

b. Artificial burrows

Providing S. erythrodactyla with burrows had a significant effect on the preference of crabs between mounds and flats. When burrows were provided in mounds and flats, significantly more crabs were found in the mounds (Chi-squared test, $P < 0.025$, and Table 5.4). The proportions of crabs in mounds and flats were not significantly different from those expected from the proportions of artificial 'burrows' provided in each microhabitat (Chi-squared test, $P > 0.50$). When burrows were provided in flats only, more crabs occurred here than in the mounds, although the difference was not significant (Table 5.4). Providing burrows did not affect the distribution of new depressions.

c. Topography and material

Because S. erythrodactyla demonstrated no significant or consistent preference between mounds and flats, no experiment was done on the roles of topography and material on habitat selection.

In summary, the only factor shown to have a significant effect on the distribution of S. erythrodactyla between mounds and flats was the presence of burrows. Because this species does not (or cannot) make proper burrows

Table 5.9. Numbers of *H. cordiformis* and their burrows in enclosed mounds and flats, with and without a second species. The second species was added 1 week before, 1 week after or simultaneously with *H. cordiformis*. Numbers of crabs and burrows have been pooled from 3 enclosures. Natural densities of 20 *H. cordiformis*, 4 *P. laevis* and 4 *S. erythrodactyla* were used. Data for *H. cordiformis* alone and with prior and subsequent addition of the other species were from Day 6 (April 1986); data for simultaneous additions were from Day 7 (May 1986). HC = *H. cordiformis*, PL = *P. laevis*, and SE = *S. erythrodactyla*.

SPECIES:		HC ALONE	WITH *P. LAEVIS*			WITH *S. ERYTHRODACTYLA*		
TREATMENTS:		NO 2ND SP.	HC THEN PL	HC & PL	PL THEN HC	HC THEN SE	HC & SE	SE THEN HC
CRABS	MOUND	43	34	25	34	44	30	44
	FLAT	7	7	12	6	3	11	5
	χ^2			5.64 (3 df)			8.52 (3 df)	
	P			> 0.10			< 0.05	
BURROWS	MOUND	60	60	42	42	56	46	47
	FLAT	11	5	9	2	5	8	6
	χ^2			5.13 (3 df)			1.91 (3 df)	
	P			> 0.10			> 0.50	

but inhabits burrows under natural conditions, the distribution of burrows probably largely determines the distribution of crabs.

Interspecific interactions

Including a second species in enclosures had very little effect on patterns observed when each species was enclosed on its own. Despite prior, simultaneous or subsequent addition (to enclosures) of P. laevis or S. erythrodactyla, H. cordiformis continued to burrow in and occupy burrows in mounds more frequently than in flats (Table 5.9). The magnitude of the difference between the numbers of crabs in mounds and flats varied among the four treatments, with somewhat greater proportions of H. cordiformis in flats when the second species was added simultaneously. This variation was significant only when S. erythrodactyla was the second species.

The distributions of P. laevis and S. erythrodactyla in the presence of another species did not become any more consistent than when tested on their own (Tables 5.10 and 5.11). Interspecific interactions, therefore, did not appear to be an important mechanism underlying the tendency of P. laevis to occur more often in flats than in mounds nor did it prove a more likely mechanism than preference (or lack thereof) resulting in the observed distribution of S. erythrodactyla under natural conditions.

Discussion

When enclosed in the absence of other species, the resulting distributions of each of the three species between mounds and flats generally reiterated patterns observed for the populations at large. In addition, the degree of variability observed for each species in enclosures was similar to

Table 5.10. Numbers of *P. laevis* and their burrows/depressions in enclosed mounds and flats, with and without a second species. The second species was added 1 week before, 1 week after or simultaneously with *P. laevis*. Because burrows/depressions of *P. laevis* are indistinguishable from those of *S. erythrodactyla*, the associated analysis of burrows/depressions was not done. Numbers of crabs and burrows/depressions have been pooled from 3 enclosures. Natural densities of crabs were used (as in Table 5.9). Data for *P. laevis* alone and with simultaneous addition of the other species were from Day 7 (April and May 1986, respectively); data for sequential additions were from Day 6 (April 1986). Abbreviations as in Table 5.9.

SPECIES:		PL ALONE	WITH *H. CORDIFORMIS*			WITH *S. ERYTHRODACTYLA*		
TREATMENTS:		NO 2ND SP.	PL THEN HC	PL & HC	HC THEN PL	PL THEN SE	PL & SE	SE THEN PL
CRABS	MOUND	8	8	6	9	9	3	7
	FLAT	3	4	5	2	3	9	5
	χ^2			1.96 (3 df)			7.73 (3 df)	
	P			> 0.50			> 0.05	
BURROWS	MOUND	7	10	7	11		N/A	
	FLAT	5	15	8	7			
	χ^2			1.14 (3 df)				
	P			> 0.50				

Table 5.11. Numbers of S. erythrodactyla and their burrows/depressions in enclosed mounds and flats, with and without a second species. The second species was added 1 week before, 1 week after or simultaneously with S. erythrodactyla. Because burrows/depressions of S. erythrodactyla are indistinguishable from those of P. laevis, the associated analysis on burrows/depressions was not done. Numbers of crabs and burrows/depressions have been pooled from 3 enclosures. Natural densities of crabs were used (as in Table 5.9). Data for S. erythrodactyla alone and with simulataneous addition of the other species were from Day 7 (May 1986); data from sequential additions were from Day 6 (April 1986). Abbreviations as in Table 5.9.

SPECIES:		SE ALONE	WITH H. CORDIFORMIS			WITH P. LAEVIS		
TREATMENTS:		NO 2ND SP.	SE THEN HC	SE & HC	HC THEN SE	SE THEN PL	SE & PL	PL THEN SE
CRABS	MOUND	5	4	5	8	5	3	8
	FLAT	7	6	6	2	6	9	4
	χ^2			4.36 (3 df)			4.25 (3 df)	
	P			> 0.10			> 0.10	
BURROWS	MOUND	5	4	8	5		N/A	
	FLAT	4	3	6	4			
	χ^2			0.04 (3 df)				
	P			> 0.50				

that seen from sampling natural populations with traps and quadrats (Chapter 3). Preference (or habitat selection) is, therefore, a likely mechanism underlying the natural distributions of crabs between mounds and flats.

Results from experiments with *H. cordiformis* were generally more consistent than for the other two species. One reason is that the distributions of this species in nature and in enclosures with natural mounds and flats were more consistent (see Chapter 3 and Table 5.1), and, therefore, deviations from these patterns were more striking when characteristics of the substratum or other factors were manipulated.

Undoubtably, the greater natural density of *H. cordiformis* (five times that of the other two species) contributed to the decreased variability in results in experiments. One or two crabs moving from one microhabitat to the other would have very little effect on the resulting distribution relative to a similar shift for *P. laevis* or *S. erythrodactyla*. Experiments (except those on crowding) used natural densities to reproduce natural conditions (see Underwood 1986), and this was considered to be more important than using greater densities in the hope of obtaining less variable results for the two grapsid species.

Crowding significantly altered the proportions of burrows of *H. cordiformis* and *P. laevis* in their preferred microhabitats. With *P. laevis*, the magnitude of the effect corresponded to the degree of crowding: at 2.5x and 5x natural density, a greater proportion of burrows were made in mounds than at natural density (Table 5.2). Displacement might have resulted from an increase in agonistic encounters in flats under crowded conditions, but little is known of the behaviour of this elusive species, and under natural conditions few intraspecific interactions were observed.

Under crowded conditions, H. cordiformis made fewer burrows per crab than crabs at natural density (Table 5.3). At 5x natural density, there were fewer burrows than crabs, indicating that some burrows housed more than one crab, at least on a temporary basis. Crabs probably cannot survive outside burrows during periods of submersion because of subtidal predators (see Chapter 7). Perhaps crabs ceased making new burrows because the substratum might have collapsed from over-excavating the sediments. Cessation of 'hole-digging' when crabs were enclosed at great density has been demonstrated for another burrowing mangrove crab, Helograpsus haswellianus (McKillup and Butler 1979). The mean maximum number of burrows (per enclosure) in the present study was observed in the 5x natural density treatment: 75 burrows (per 0.45 m^2). Perhaps this represented the maximum load the substratum could still support.

Presence of burrows, topography, material and disturbance were all shown to affect habitat selection. Only two studies have experimentally examined the preference of these three species to different types of substratum, and both were done in the laboratory. Yates (1978) tested preferences between fine substratum from the seaward zone and coarser substratum from the midmangrove and landward zones, and also preference for waterlogged versus well-drained substratum. H. cordiformis and P. laevis preferred waterlogged sediments regardless of their origin (or composition); S. erythrodactyla demonstrated a preference for coarse, waterlogged sediments.

Griffin (1971) did similar experiments using fine, medium and coarse substratum. He obtained conclusive results only for H. cordiformis which preferred the intermediate type of sediments. Because the relationship between origin of the substratum used in his experiments and the distribution of crabs in mangrove swamps was not disclosed, the results cannot be compared with those of the present study.

For all species, providing artificial burrows in only one microhabitat led to an increase in the proportions of crabs occurring there. The final pattern of distribution of H. cordiformis still reflected a preference for mounds, but the weak preference of P. laevis for flats was shifted to mounds when burrows were provided there only (Table 5.4). Providing burrows in only flats resulted in more S. erythrodactyla occurring there than in mounds. The importance of extant burrows in habitat selection was further demonstrated by all species occupying mounds and flats in proportion to the numbers of artificial burrows provided in each microhabitat.

In nature, these effects might be limited by the defence of burrows by the occupant. Of the three species in this study, H. cordiformis is the only one that makes and maintains proper burrows (i.e. deep tunnels extending below the surface). Because they prefer mounds (and, in fact, build these mounds as a by-product of their excavations; see Chapter 6), the density of burrows is much greater in mounds than flats (approximately 13 per m^2 in mounds vs. 5 per m^2 in flats, from 10 quadrats). Despite the greater availability of burrows in mounds, neither P. laevis nor S. erythrodactyla are more abundant in this microhabitat. Because H. cordiformis defend their burrows against other crabs, it is possible that the two grapsids are prevented from taking over burrows in mounds or search for unoccupied burrows in flats.

The experiments revealed that when H. cordiformis was added before another species (and was, therefore, able to make and occupy burrows in mounds), four times more P. laevis and S. erythrodactyla settled into burrows in mounds than in flats (Tables 5.10 and 5.11). These represented greater proportions than those in enclosures receiving these species before or simultaneously with H. cordiformis. The creation of burrows by H. cordiformis, therefore, somewhat enhanced their occupation by the grapsids. Defence of burrows did not, therefore, contribute to patterns of distribution of P. laevis or S. erythrodactyla.

Although several other studies with crabs have inferred that observed distributions were the result of preference, few have actually tested this or any other mechanism. The overall conclusion from the experiments of the present study is that H. cordiformis are found primarily in mounds and P. laevis tend to be found primarily in flats because they choose the different microhabitats, and S. erythrodactyla are found in both microhabitats because they have no significant or consistent preference for either.

CHAPTER 6. EFFECTS OF HELOECIUS CORDIFORMIS ON THE SUBSTRATUM IN MANGROVE SWAMPS (SUMMARY OF PUBLICATION IN APPENDIX 6.1)

In the previous chapter, a significant effect of the nature of the substratum on the distribution of H. cordiformis was demonstrated: crabs preferred to occupy mounds rather than flats (Chapter 5). The crabs might also have significant effects on the nature of the substratum because H. cordiformis excavate burrows and sift through the sediments while feeding. The repeated deposition of material from burrows onto the surface close to the entrance could easily result in the creation of mounds. The undulating topography of the substratum might, therefore, be related to the burrowing activities of H. cordiformis.

The apparently coarser composition of sediments in mounds relative to flats might also reflect bioturbation by crabs. The sediments at the surface in flats seemed to be composed primarily of fine silts and clays, but the substratum below the surface was much coarser. By excavating burrows in flats, H. cordiformis would, therefore, deposit coarse sediments onto the fine material in flats, resulting in a coarser distribution of grain-sizes (texture) at the surface.

Because H. cordiformis ingest living and non-living organic matter associated with the substratum, areas foraged by these crabs should have a smaller abundance of organic matter and microalgae than areas not subject to this activity. An alternative is that the activities of crabs stimulate algal and microbial growth by the excretion of inorganic nutrients and by the increased penetration of oxygen associated with mechanical disturbance of the sediments (Gosselink and Kirby 1974; Hoffman *et al.* 1984; Montague 1980). Hylleberg (1975) referred to this process as 'gardening'.

Experiments to examine these propositions are described in detail in Appendix 6.1; the major results are summarised here.

In experimental enclosures with and without crabs, the percent cover of mounds of various heights was calculated from stereophotographs after 14 and 129 days (see Appendix 6.1, Figure 1). After only two weeks, the proportion of substratum at several levels of contouring was significantly greater in enclosures with crabs than in those without crabs (Appendix 6.1, Figure 2). Differences in topography between the two treatments became even more striking after 129 days. The burrowing activity of *H. cordiformis* was responsible for the increased relief of substrata in experimental enclosures and may be responsible for the topographic complexity of the floor of the swamp.

Crabs also had a significant effect on the texture of sediments. The substratum at the surface in enclosures with crabs was composed of a greater proportion of sand (Appendix 6.1, Figure 3).

Algae were less abundant where there were crabs (Appendix 6.1, Table II), probably because crabs consume this material. *H. cordiformis* did not affect the abundance of organic matter. Clearly, however, crabs had a significant effect on the physical and biotic characteristics of the substratum in mangrove swamps.

CHAPTER 7. BEHAVIOURAL ASPECTS OF THE ECOLOGY OF *H. CORDIFORMIS*

INTRODUCTION

H. cordiformis is similar to its ocypodid relatives, the fiddler and ghost crabs, in displaying a variety of easily observed behaviours. Activities seen on the surface have been described in detail for the fiddler and ghost crabs and for other ocypodids by Christy (1978, 1982a, b), Christy and Salmon (1984), Hyatt (1977), Hyatt and Salmon (1978), Lighter (1974), Murai et al. (1982), Nakasone (1982), Salmon (1984), Salmon and Hyatt (1983), Valiela *et al*. (1974), Wada (1985), and many others (see reviews by Barnwell 1968, Crane 1975, and Montague 1980 for earlier papers). Unlike the literature for the fiddler and ghost crabs, which is rich in qualitative and quantitative studies, the few studies on local species of mangrove or estuarine crabs have examined the behaviour only qualitatively (Cameron 1966; Griffin 1965, 1968, 1971; Musgrave 1929; Ward 1928).

Previous studies (e.g. Griffin 1965, 1968) and casual observations throughout my study have suggested that the number of crabs active on the surface, the prevalence of certain behaviours and the general level of activity might all be subject to daily and/or tidal rhythmicity. The importance of these, in addition to semilunar effects, on a variety of behaviours has already been demonstrated in many species of fiddler crabs. Crane (1958, 1975) observed an increase in waving by male *Uca vocans* in Fiji and *U. thayeri* in Trinidad just prior to sunset (daily rhythm). Feeding was the first activity many species engaged in after the tide ebbed; social behaviour peaked during the middle of the period of low tide; and a second peak of feeding combined with maintenance of burrows occurred during the last 1-2 hours before submersion by the incoming tide (tidal rhythm). She also noted that on many shores maximum social activity took place fortnightly, beginning 1-2 days after new and full moons (semilunar rhythm; Crane 1975). This third type of rhythm (representing a synergistic interaction between daily and tidal rhythms) has been demonstrated for the release of larvae by female U. pugilator (Christy 1978) and the construction of burrows by male U. terpsichores (Zucker 1974). These are but a few examples of many studied in the laboratory and field (under completely natural conditions or semi-natural conditions, i.e. those utilising outdoor crabberies).

With respect to the number of crabs seen on the surface, an understanding of these effects is crucial to a correct interpretation of results from the sampling programmes for the distribution and abundance of H. cordiformis (Chapters 3 and 4). Sampling involved counting crabs emerging from burrows within a 10-minute period of observation. If the number of crabs emerging varied significantly throughout the day and/or period of low tide, then the timing of sampling might have produced spurious results in the assessment of day-to-day or seasonal effects. An extreme example would be an examination of seasonal effects by sampling crabs in spring and summer during the day and in autumn during the night, when this species is virtually absent from the surface during nocturnal low tides (Hutchings and Recher 1974; pers. obs., this study). Thus, two objectives of this chapter are to examine the importance of time-of-day and tidal phase (early, middle and late periods within a given low tide) relative to the number of crabs emerging onto the surface. These numbers were considered indicative of the general level of activity of the population. A second criterion, the numbers of open burrows of H. cordiformis, was also used to estimate the general level of activity. The relationship between these two variables (the number of crabs emerging and the number of open burrows) was examined and is described in this chapter.

A third objective is to describe the effects of these factors on the prevalence of certain behaviours (e.g. feeding, maintenance of burrows, intraspecific interactions, etc.) in addition to the general level of activity. These factors were also examined with regard to the proportion of time spent at various distances from the burrow while engaged in these behaviours. In addition, the minimum and maximum distances at which these activities were observed were also determined.

Sex was examined as a factor that might influence the prevalence of certain behaviours. Studies on Uca have demonstrated that only males initiate courtship (Christy 1982b; Crane 1975; Zucker 1983). Reproductive males of many species occupy burrows in distinct areas for courtship. Females wander through these areas and males display to attract females into their burrows where copulation occurs. Another indication that sex affects patterns of activity is that female fiddler crabs only rarely engage in combat over ownership of burrows (Crane 1975). Most episodes of courtship in H. cordiformis involve a male approaching a female at her burrow and courting and coupling with her there, frequently on the surface; therefore, courting males could be expected to move further and/or more frequently from their burrows than conspecific females. Distances moved by male and female H. cordiformis were measured to examine the effect of sex on mean distances traversed and number of excursions from the burrow. The collection of these data also allowed an examination of the relationship of period of activity to the frequency and extent of excursions.

Factors correlated with tidal zone might be important in determining the nature and prevalence of certain behaviours. The most obvious effect of zone is a shorter period of emersion (and therefore a shorter period available for activity on the surface) for crabs living low on the shore than crabs living higher on the shore. The substratum in the midmangrove zone differs in several ways from that in the landward zone (e.g. density of peg roots, particle size distribution of soil, extent of drainage, etc.), and this might affect the proportion of time spent maintaining burrows, feeding, etc. The possible effects of these and other differences between the two zones were considered important enough to merit examination of tidal zone as a factor in the analysis of behaviour.

H. cordiformis vigorously defend their burrows (Griffin 1965, 1968; Ward 1928; pers. obs). The success of this behaviour, in terms of the duration of ownership of a particular burrow (or fidelity), was evaluated, and the results are also described in this chapter. Crane (1975) suggested that burrows of fiddler crabs were typically maintained by individuals for only a few days, although she recorded a few examples of crabs keeping the same burrow for up to 6 months and many more examples of crabs changing burrows at least once during a given period of low tide.

The burrow is the centre for most of the behaviours exibited by H. cordiformis. In Uca spp., it is the exclusive site of acoustical signalling by males, extrusion of eggs by females and the usual site for courtship and copulation (Crane 1975; Salmon 1983). The potential role of the burrow as a refuge from subtidal predators, however, had not been quantitatively examined for either the fiddler crabs or the local species of mangrove crabs. Examination of gut contents from the toadfish, Tetractenos hamiltoni (Gray and Richardson)(Gum 1985), indicated that this fish preys on crabs and snails. T. hamiltoni is also abundant in the mangrove forest during periods of submergence (Gum 1985; pers. obs). Remaining in burrows during high tide was, therefore, predicted to lead to reduced mortality of H. cordiformis from predation by toadfish. Results from an experimental test of this prediction are also discussed in this chapter.

BEHAVIOURAL REPERTOIRE OF H. CORDIFORMIS

Analysis of the activity patterns of H. cordiformis involved the four most frequently observed behaviours of this species: feeding, maintenance of burrows, pausing and forming mud balls (Griffin 1968). Each of these behaviours, described with others below, is continuous, lasting at least 15 seconds and usually lasting several minutes.

Normal Feeding: Crabs stand in one place, walk slowly or intersperse one with the other as they pick up sediment with either chela (usually alternating between left and right). This sediment is passed to the mouth where detritus and micro-organisms are extracted by the setose mouthparts. As food is extracted a small droplet of wet, processed sediment collects at the base of the third maxillipeds. This droplet is removed by a chela, drops to the ground or, more rarely, is pressed onto the substratum as the crab leans forward (Griffin 1968; pers. obs.)

Displacement Feeding: Crabs go through motions identical to normal feeding (i.e. moving the tips of the chelipeds from the substratum to the mouth), but no material is actually brought to the mouth and feeding pellets do not develop. It is usually demonstrated by former owners of burrows which have recently been evicted from their burrows by aggressive wanderers and are in the process of finding new burrows. It is also observed in some crabs wandering over the surface and not returning to a burrow.

Walking: Crabs walk sideways and are usually simultaneously involved in some other activity, such as feeding, forming mudballs, or challenging owners of burrows, rather than just 'strolling about'.

Pausing: Crabs stand nearly motionless in or near the entrance to their burrow and may remain so for many minutes. Griffin (1968) described such behaviour as 'burrow defence' because he never saw a crab with this stance challenged by another crab. On one occasion, he saw one crab maintain this posture for 41 minutes. I have frequently seen crabs doing this for 10-15 minutes. Occasionally the abdomen is lowered for a portion of the duration of the stance.

Forming Mud Balls: Crabs pick up sediment and hold it between the third maxillipeds, adding new material until the ball of sediment reaches 10-15 mm in diameter. This is usually done while walking or, at least, involves a moderate amount of walking, and is rarely done adjacent to the burrow. After the sediment has accumulated into a large ball, the crab carries the ball back to the burrow, pauses at the entrance while the ball is disengaged from the mouthparts, and then takes the ball down the burrow. On rare occasions the ball is deposited adjacent to the entrance of the burrow. Griffin (1968) described this as a behaviour involved with maintaining the inside of the burrow. Because the burrows of H. cordiformis are not always lined with mud, Griffin's evaluation may be incorrect. Until observations are made on H. cordiformis after it takes these balls into its burrow, one cannot dismiss other possible functions, e.g. providing food while the crab remains within its burrow during high tide (Nakasone 1982 and Salmon 1984, for Uca vocans; Wada 1985, for Dotillopsis brevitarsis).

Plugging Burrows: Before nightfall or inundation by the advancing tide, crabs plug their burrows with substratum. The material can be formed and brought to the burrow in a manner similar to forming mud balls (described above), the crab sealing off the entrance behind it as it descends into its burrow. Alternatively, the crab can stand in the entrance and with the left or right legs scrape up mud from outside the burrow and pull this material over like a blanket which is then tamped into place. The third method involves plugging the burrow from within, using substratum from inside the burrow. In this case, the plug usually rests 5-20 mm below the entrance whereas the first two methods result in the burrow being almost indistinguishable from the surrounding substratum.

Maintenance of Burrows: This behaviour has several forms. In most cases it involves bringing balls of mud to the surface (one at a time) and depositing them adjacent to the entrance, packing them into a wall around or next to the entrance or rolling them up to 20 cm away from the burrow, usually while on a feeding excursion. Other maintenance involves tamping or pressing the walls of the entrance upon entering or leaving the burrow.

There are probably other maintenance and repair activities which occur entirely within the burrow and are unobservable from the surface.

Displays With the Chelae: Most of these displays occur at or near a burrow and are involved in defence of the burrow or courtship. When a wandering crab approaches another's burrow, the owner will dash to its burrow and usually assume one of several postures of increasing intensity: i) chelipeds held forward, half-flexed, with tips touching the ground, ii) chelipeds and fingers held forward toward approaching crab, or iii) chelipeds moved out laterally, suddenly jerked down and back to the original position in front of the body, and repeated several times in succession (= waving). Waving is also used in courtship, but in this context it has been observed only in summer (Griffin 1968). Females frequently reject courtship by males by waving them off.

Lunges Toward Another Crab: Sometimes the owner of a burrow will lunge toward an intruder while displaying the chelipeds as above. This usually results in warding off the intruder. Females may also lunge at courting males when rejecting these advances.

Fighting: Fighting can occur between males, between females or between a male and female, and is most prevalent in summer. Interspecific fights have not been observed (Griffin 1968; pers. obs.). Escalation of displays to aggressive combat usually involves pushing with the chelipeds and/or grasping the legs (or less frequently the body) of the opponent until one crab retreats. Most fights concern ownership of the burrow and occur near the burrow, either between the owner of a burrow and a wanderer or between neighbouring owners. Two factors influencing the outcome of such fights are relative body size and ownership, large body size and ownership conferring advantage (Griffin 1968 and Hyatt and Salmon 1978, for *Uca pugilator*). Griffin (1968) reported that in 11 of 12 closely studied fights observed in a 'crabbery' of *H. cordiformis*, the winner was the larger crab. During one period of observation, the intruder won only 1 fight of 10 observed. My observations correlate well with these. Because most of my quantitative observations were made during late autumn, when fighting is not frequent, only a few episodes were seen.

Other Defensive Behaviour: In many encounters between the owner of a burrow and a threatening intruder, the owner retreats and wedges itself into the entrance to the burrow. Sometimes the crab blocks the entrance with a chela (Nakasone 1982, for *Uca vocans*). In this position, it can usually prevent an intruder from entering or grasping it, and the intruder wanders off, with or without first attempting to dislodge the owner. On two occasions during the three and a half years of this study, an intruder reached into the burrow, grasped and removed the owner and took over the burrow. In both cases the intruder was much larger than the owner and the burrow had to be enlarged to accommodate the new owner.

Griffin (1968) described the occurrence of large numbers of crabs simultaneously engaged in 'aggressive wandering', especially among large males. I have never seen more than 2-3 such wanderers entering 0.25 m^2 sites during 15-30 minute periods of observation and challenging owners of burrows, even during summer.

Courtship: Although, during summer, waving displays by males are involved in courtship, this behaviour was not observed during the sampling in autumn. Courtship always involved a male approaching a female at her burrow or in the entrance to her burrow. The male rapidly tapped the carapace or legs of the female (= tickling) and/or 'fed' off her (the chelae picking at her carapace or legs and moving to the mouth without food). The apparent tickling behaviour involving a female deep within the entrance might have been acoustical drumming on the walls of the burrow, a behaviour observed in many species of fiddler crabs (Crane 1975; Salmon 1984); however, from a distance and without acoustical recorders this possiblity could not be confirmed.

Coupling: On six occasions, courtship was succeeded by coupling outside the entrance to the female's burrow. The male, facing the female, enclosed the female within his chelipeds and both crabs remained relatively still for several minutes, although the abdomen of one or both could be seen to be lowered and the male sometimes picked at the carapace of the female. It was not possible to determine if successful copulation had occurred. Copulation may occur in the burrow, but I did not examine this possibility.

More detailed descriptions of these and other behaviours, including postures and movements of the body and limbs, can be found in Griffin (1968).

A. TIDAL AND DAILY VARIABILITY IN THE APPARENT ABUNDANCES OF CRABS

Methods and Materials

Examination of tidal and daily variability in the numbers of crabs emerging from burrows (i.e. apparent abundance) consisted of two phases. The first was to test if *H. cordiformis*, *P. laevis* and *S. erythrodactyla* are primarily nocturnal or diurnal species. Hutchings and Recher (1974) suggested the latter. The second phase was to determine if apparent abundance of *H. cordiformis* varied significantly from the early to late periods during diurnal emersion. Because relatively few *P. laevis* and *S. erythrodactyla* emerge during diurnal censuses, this second phase focused on *H. cordiformis* only.

Investigation of differences between diurnal and nocturnal apparent abundances was done in the midmangrove zone at Careel Bay and utilised the standard method of direct visual counts. Crabs emerging within a 0.25 m^2 quadrat within a 10-minute period after emergence of the first crab were counted during low tides during daylight and after dark on the same day (at least two hrs after emersion). This was done on two days during neap tides in summer: 14 December 1984 and 16 January 1985. At night, head torches had to be used to see crabs on the substratum. Because the behaviour of several nocturnally-active marine decapods has been shown to be affected by white light more than red light (e.g. Lipcius and Herrnkind 1982), half of the nocturnal observations were done with red light and half with white. Light of either colour would not stimulate or suppress the first emergence of *H. cordiformis*, because the burrows are plugged until first emergence, but crabs emerging from already opened burrows might be affected. The nature of the

Table 7.1. Analysis of variance of the number of crabs emerging at night (on 16 January 1985) from burrows in mounds and flats when sites were illuminated by red or white light. Data were transformed to $\sqrt{x+1}$, and Cochran's test was not significant ($P > 0.05$); $n = 6$ quadrats. All 3 species of crabs were sampled.

SOURCE	DF	MS	F	P
Colour of light	1	1.00	3.23	> 0.05
Microhabitat	1	0	0	> 0.50
Species	2	2.13	6.87	< 0.01
C.L. x MH	1	0.03	0.10	> 0.50
C.L. x SP	2	0.64	2.06	> 0.10
MH x SP	2	1.00	3.23	< 0.05
C.L. x MH x SP	2	0.05	0.16	> 0.50
Residual	60	0.31		

Mean number of crabs emerging (+ S.E.) per quadrat. Data are untransformed:

	RED LIGHT	WHITE LIGHT
H. cordiformis		
mound	0.33 (0.33)	1.00 (0.68)
flat	0	0
P. laevis		
mound	1.67 (1.12)	0.50 (0.34)
flat	3.00 (1.10)	2.00 (0.34)
S. erythrodactyla		
mound	3.67 (1.38)	1.83 (0.91)
flat	3.17 (1.80)	0.67 (0.67)

effect, if it existed, was predicted to be stimulatory for white light because this most closely resembles natural daylight (when this species is active). Analysis of the mean numbers of H. cordiformis, P. laevis and S. erythrodactyla emerging at night indicated no significant effect of the colour of illumination used (Table 7.1).

During the nocturnal census on 14 December 1984, 6 mounds and 6 flats were sampled using red lights only; subsequent sampling with white light could not be done due to rain. On 16 January 1985, 6 mounds and 6 flats were sampling using each type of light (i.e. a total of 12 mounds and 12 flats). For the final analyses of effects of Time of day (day vs. night) on the apparent abundances of crabs, data from sampling with red light only were used to balance the number of replicates from each census. On 16 January, the numbers of open burrows per quadrat were also counted during the diurnal and nocturnal census to provide a different index for evaluation of the general level of activity for all species.

To examine differences in the numbers of H. cordiformis emerging from burrows during the early, middle and late periods of diurnal emersion, visual counts were commenced within 30 minutes after emersion or dawn (whichever occurred first). This allowed recording of the beginning of activity on the surface. Because crabs begin to emerge in response to two different environmental events - dawn (if emersion occurs during the night) or emersion (if this occurs after dawn) - the timing of censuses was set relative to the type of environmental event preceding the start of activity. For pre-dawn occurrences of emersion, the 'early' period of activity was sampled from 0.50 to 1.75 hrs after dawn; the 'middle' period from 2.50 hrs after dawn to 2.50

Table 7.2. Analysis of variance of the numbers of *H. cordiformis*, *P. laevis* and *S. erythrodactyla* emerging from burrows in mounds and flats during 2 days and nights of sampling. Data were transformed to ln (x+1), and Cochran's test was not significant ($P > 0.05$). Census = 14 December 1984 vs. 16 January 1985) and Time of day = day vs. night; $n = 6$ quadrats.

SOURCE	DF	MS	F	P
Census	1	0.94	3.48	> 0.05
Time of day	1	2.31	8.56	< 0.01
Microhabitat	1	0.86	3.19	> 0.05
Species	2	0.65	2.41	> 0.10
C x T	1	0	0	> 0.50
C x MH	1	0.13	0.48	> 0.50
C x SP	2	0.45	1.67	> 0.10
T x MH	1	2.95	10.93	< 0.01
T x SP	2	9.26	34.30	< 0.001
MH x SP	2	12.29	45.52	< 0.001
C x T x MH	1	0	0	> 0.50
C x T x SP	2	0.03	0.11	> 0.50
C x MH x SP	2	0.14	0.52	> 0.50
T x MH x SP	2	6.77	25.07	< 0.001
C x T x MH x SP	2	0.22	0.81	> 0.25
Residual	120	0.27		

hrs before submergence; and the 'late' period during the last 1.25 hrs before submergence. On several days, additional sampling was done outside these periods. A census of apparent abundance during each period consisted of counting crabs emerging from burrows (in mounds only) in five quadrats (0.25 m^2) per period.

When emersion occurred after dawn, the 'early' period was censused by counts in five quadrats from 0.50 to 1.75 hrs after emersion; the 'middle' period from 2.50 hrs after emersion to 2.50 hrs before dusk (or submergence); and the 'late' period during the last 1.25 hrs before dusk (or submergence). Additional samples were taken on several days.

Results

1. Diurnal vs. nocturnal apparent abundances

The apparent abundances of all three species were analysed with respect to Day of census (14 December 1984 vs. 16 January 1985), Time of Day (day vs. night) and Microhabitat (mound vs. flat). The 4-factor analysis of variance demonstrated significant interactions of Species with Time of day and Microhabitat (Table 7.2); therefore, data were re-analysed for each species separately. There was no significant difference between results from each Day of census, and these were pooled in subsequent analyses.

H. cordiformis were shown to be strongly diurnal, emerging from burrows only in very small numbers during the night (Table 7.3). Unresolvable heterogeneity among variances resulted from a wide range in the numbers of crabs emerging from burrows in mounds during the day on 16 January 1985; there was less variance on 14 December 1984. The relatively great F-ratios

Table 7.3. Analysis of variance of the numbers of crabs emerging from burrows in mounds and flats during 2 days and nights of sampling. For each analysis, data were transformed to ln (x+1), as in Table 7.2, but Cochran's test was still significant ($P < 0.05$; see text). Time = day vs. night; Microhabitat (MH) = mound vs. flat; n = 6 quadrats. Means below table are the number of crabs (untransformed) per 0.25 m^2 quadrat.

		H. CORDIFORMIS			*P. LAEVIS*			*S. ERYTHRODAC.*		
SOURCE	DF	MS	F	*P*	MS	F	*P*	MS	F	*P*
Time	1	19.2	192.0	< 0.001	1.1	3.7	> 0.05	0.5	1.3	> 0.10
MH	1	18.5	185.0	< 0.001	6.9	23.0	< 0.001	0	0	> 0.50
T x MH	1	15.9	159.0	< 0.001	0.3	1.0	> 0.25	0.2	0.5	> 0.25
Resid.	44	0.1			0.3			0.4		

MEANS (+ S.E.):

	H. CORDIFORMIS	*P. LAEVIS*	*S. ERYTHRODAC.*
Mounds - Day	12.1 (1.7)	0.2 (0.1)	1.4 (0.4)
- Night	0.2 (0.2)	1.3 (1.1)	2.8 (1.0)
Flats - Day	0.2 (0.1)	2.1 (0.5)	1.7 (0.5)
- Night	0	2.8 (0.9)	2.3 (1.2)

for Time of day, Microhabitat and their interaction suggest that categorising H. cordiformis as mound-dwelling, diurnal animals is probably valid, despite the heteroscedasticity.

P. laevis were active on the surface during diurnal and nocturnal low tides, with similar numbers of crabs emerging at each time (Table 7.3). The only significant factor was Microhabitat, which indicated the prevalence of this species in flats relative to mounds.

The numbers of S. erythrodactyla emerging from burrows during diurnal and nocturnal low tides were similar for mounds and for flats (Table 7.3).

The second index for assessing the general level of activity on the surface was the density of open burrows. For H. cordiformis, an open burrow usually indicates that the owner has not yet terminated its activities on the surface (or that the burrow is unoccupied). The same cannot be said for burrows of the other two species. Crabs rarely emerged from burrows typical of the two grapsids (i.e. burrows with oval or irregularly-shaped entrances), and neither species plugs the burrow at the end of its period of activity. Burrows were more prevalent in mounds than flats, especially during the day (Table 7.4). This result is not surprising because the majority of burrows in mounds belong to H. cordiformis which remain in their plugged burrows during nocturnal periods of emersion.

2. Variation in apparent abundances within diurnal periods of emersion

Neither Period during emersion nor Timing of emersion (pre-dawn vs. post-dawn) had a significant effect on the apparent abundance of H.

Table 7.4. Analysis of variance of the number of open burrows in mounds and flats during the day and night of 16 January 1985. Time of day = day vs. night. Data were transformed to $\sqrt{x+1}$, and Cochran's test was not significant ($\underline{P} > 0.05$); $\underline{n} = 6$ quadrats.

<u>SOURCE</u>	<u>DF</u>	<u>MS</u>	<u>F</u>	<u>P</u>
Time of day	1	3.21	35.67	< 0.001
Microhabitat	1	6.36	70.67	< 0.001
T x MH	1	2.37	26.33	< 0.001
Residual	20	0.09		

Mean number of open burrows per quadrat (+ S.E.). Data are untransformed:

	MOUND	FLAT
Day	15.33 (1.28)	4.67 (0.56)
Night	6.17 (0.60)	4.17 (0.40)

note: Time of day, Microhabitat and T x MH were also significant in the analysis of numbers of <u>H. cordiformis</u> emerging from burrows (Table 7.3).

cordiformis (Tables 7.5 and 7.6). During the late period of activity, crabs responded more synchronously to imminent submergence than to nightfall. For example, all crabs entered and plugged their burrows before diurnal submergence; however, on 16 October 1985, crabs were still on the surface one hour after dusk (Figure 7.1). On days when activity on the surface was terminated by submergence, apparent abundances during the late period were, therefore, less than on days when activity was (eventually) terminated by nightfall (viz. counts for last five quadrats on 10 or 11 October 1985 vs. last 5 quadrats on 15 or 16 October). Because this difference in response is relevant only for the late period, this may have led to the significant interaction between day of Census and Period in the analysis of variance (Table 7.5). Also, on days which had at least 9 hours of diurnal emersion, crabs did not immediately begin to emerge after dawn or emersion (Figure 7.1). This might have affected the apparent abundances during the early periods. When the period of emersion was shorter than 9 hours, perhaps the limited amount of time for feeding, forming mud balls and other activities provided an impetus for an earlier start of activity on the surface. When fewer than three hours of diurnal emersion occurred, very few crabs emerged from burrows.

The apparent abundances of crabs throughout the middle period of emersion were fairly similar (Figure 7.1). Because sampling of crabs for analyses of distribution and abundance (Chapter 3) was always done within this period, results were probably not affected by sampling at different times during the period of diurnal emersion.

Table 7.5. Analysis of variance of the number of *H. cordiformis* emerging from burrows during the early, middle and late periods of emersion. Timing of emersion = pre-dawn vs. post-dawn, and Census = 3 days for pre-dawn and 3 days for post-dawn emersions. Heterogeneity of variances was not resolvable by transformation of data, but Cochran's test on untransformed data was not significant at $P = 0.01$; this probability was used to detect significance in the analysis. $n = 5$ quadrats per period, on days which had at least 6 hrs of diurnal emersion.

SOURCE	DF	MS	F	P
Timing of emersion	1	821.10	7.31	> 0.05
Census(Timing)	4	112.22	19.28	< 0.001
Period	2	93.08	3.22	> 0.05
T x P	2	65.23	2.26	> 0.10
C x P	8	28.91	4.97	< 0.001
Residual	72	5.82		

Table 7.6. Mean number of *H. cordiformis* per quadrat (+ S.E.) emerging from burrows during the early, middle and late periods of emersion. Data are untransformed. SNK tests were done at the $P = 0.01$ level (see Table 7.5).

TIMING OF EMERSION & DATES OF CENSUSES	PERIOD DURING EMERSION			SNK TESTS ON PERIODS
	EARLY	MIDDLE	LATE	
Pre-Dawn:				
7 Oct 85	4.20 (1.74)	5.60 (0.87)	0.60 (0.60)[1]	E = M = L
9 Oct 85	0	5.20 (0.58)	2.60 (1.03)[1]	E = M = L
10 Oct 85	0	9.20 (1.07)	0.40 (0.25)[1]	E = L < M
SNK Tests on Censuses	7 = 9 = 10 Oct	7 = 9 = 10 Oct	7 = 9 = 10 Oct	
Post-Dawn:				
11 Oct 85	5.20 (2.22)	7.20 (0.80)	2.00 (1.38)[1]	E = M = L
15 Oct 85	14.40 (1.29)	9.40 (0.75)	12.40 (0.51)[2]	E = M = L
16 Oct 85	10.20 (0.97)	11.80 (0.92)	9.80 (1.56)[2]	E = M = L
SNK Tests on Censuses	11 < 16 < 15 Oct	11 = 15 = 16 Oct	11 < 15 = 16 Oct	

[1] Activity on surface terminated by diurnal submergence.

[2] Activity on surface terminated by night-fall (or nocturnal submergence).

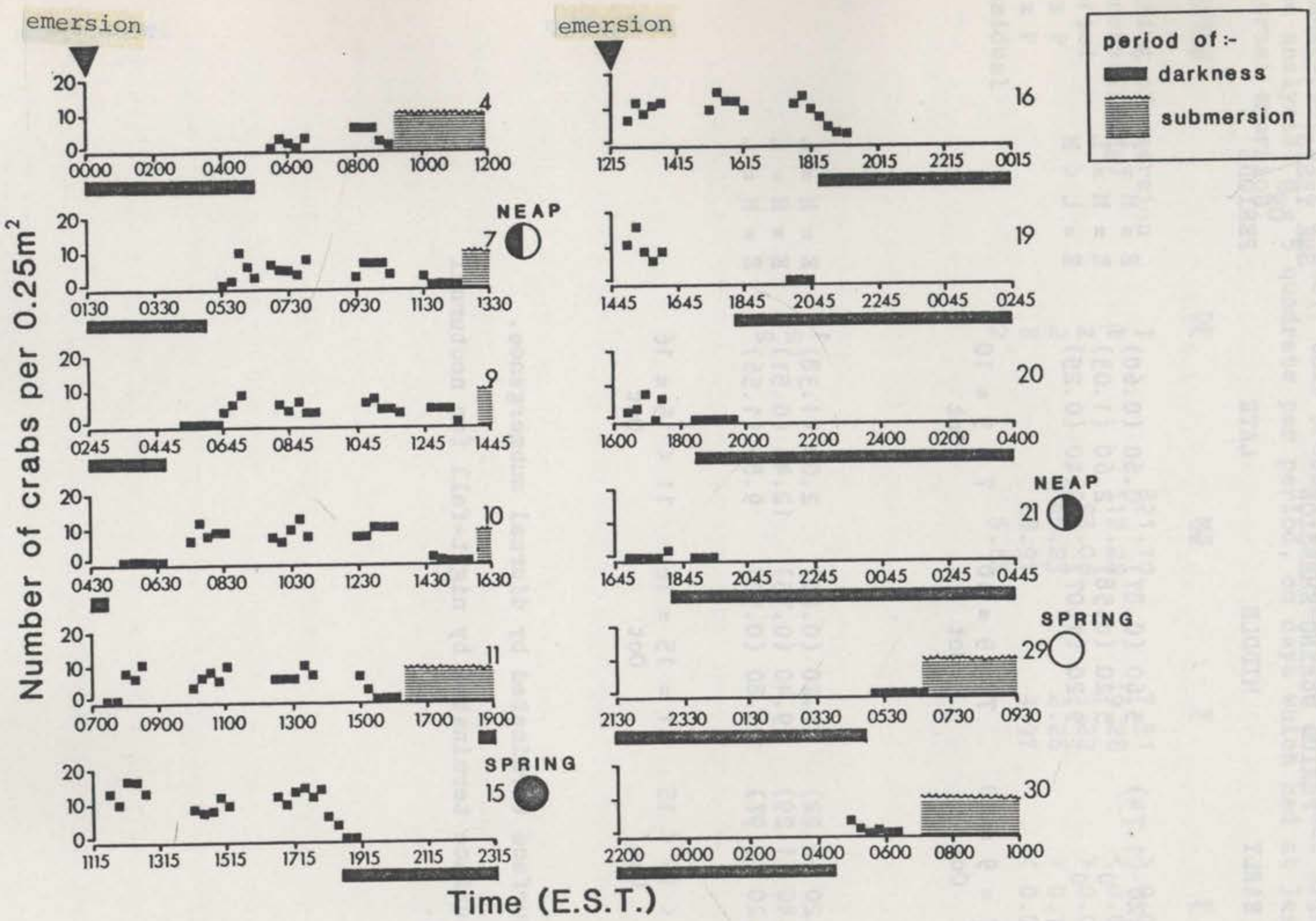

Figure 7.1. Numbers of *H. cordiformis* per 0.25 m^2, emerging from burrows at various times during diurnal emersion. Dates in October, 1985, are indicated to the right of each graph.

Discussion

Of the three species of crabs, only H. cordiformis showed a significant difference in its apparent abundance between diurnal and nocturnal periods of emersion. Although no mechanisms underlying this pattern were examined, several models merit investigation. Perhaps the activities necessary for daily maintenance and survival (e.g. feeding and repair of burrows) can be completed during a single period of emergence each day, and if this is accomplished during daylight hours, a second period of activity at night is unnecessary and not worth the risks associated with emergence (e.g. predation, loss of burrow, etc.). Defence of burrows might be more difficult at night because wanderers (which do not own burrows) would not be as visible and might be able to get closer to another crab's burrow without detection. It might also be more difficult to navigate back to a burrow at night. Behaviours associated with defence and courtship involve various displays, and these would not be as visible at night as during the day.

Aspects of this model might also explain the patterns of activity for P. laevis and S. erythrodactyla which are omnivores which obtain food by predation and scavenging. Their food, therefore, is not as ubiquitous nor as accessible as that of H. cordiformis (which extract algae, detritus and microorganisms from the sediments). Perhaps they need to be active during each period of emersion to satisfy their daily nutritional requirements.

P. laevis and S. erythrodactyla do not defend burrows to the extent done by H. cordiformis, and they make more distant excursions and do not always return to the same burrow. Also, intraspecific interactions, especially those involving displays with the chelae, are not as prevalent for the grapsids as for H. cordiformis. The importance of daylight, with respect to greater visibility of threatening crabs, might therefore be less for the grapsids which are also active at night.

Analyses of apparent abundances of H. cordiformis during the early, middle and late periods of emersion indicated a significant interaction between Days and Periods. One explanation for this interaction is that the end of activity on the surface is more precise relative to submergence than to nightfall. The adverse consequences of not responding quickly to each of these environmental events are much more severe for periods of activity terminated by submergence than for those terminated by nightfall. Crabs not entering burrows shortly after submergence will probably be eaten by subtidal predators (see Section D, this chapter). Crabs not entering their burrows by nightfall might, at worst, lose their burrows and have to engage in intraspecific disputes to find other burrows. The impetus to terminate activity on the surface, therefore, is more urgent before submergence than before nightfall. This might explain the differences in apparent abundances during the late period of emersion when two different environmental events 'trigger' the end of activity on the surface.

B. TEMPORAL AND SPATIAL PATTERNS OF ACTIVITY

Methods and Materials

The frequency and duration of certain activities of *H. cordiformis* were examined relative to time of day and tidal phase on the east shore of Woolooware Bay. Observations were made in two broad tidal zones, the midmangrove zone and the landward zone (described in Chapter 2). The seaward zone was omitted for several reasons. The greater height and density of peg roots would have obscured crabs from view in a larger portion of the observational areas than in the upper two zones. Also, peg roots in the seaward zone were usually covered with a thicker growth of filamentous algae, exacerbating this problem. Because smaller crabs are more difficult to follow (and to sex) than larger crabs, these behavioural observations were limited to crabs of medium to large size (minimum carapace length approximately 10 mm). Most crabs in the seaward zone are generally smaller than this (see Chapter 3).

1. Recording behaviours and positions of crabs

Two methods were used to record behaviour and positions of crabs relative to their burrows: direct observation and videotaping. Both methods involved the initial production of a map of all the open burrows in an area of approximately 40 cm x 40 cm. Only sites with at least 6 open burrows were selected. Other than this criterion, sites were selected haphazardly. Each burrow on the map was assigned a letter which later also identified the owner after emergence of the crab. Distances between burrows were measured after the period of observation.

After a map was produced, I sat approximately 1-1.5 m away from the site and waited for crabs to begin emerging (usually within 5-10 minutes). The time of initial emergence was noted for each crab, in addition to the sex and relative size (medium 8-12 mm and large > 12 mm carapace length). The colour of the chelae and unusual features (e.g. a missing chela or chelae of different sizes or colours) were recorded to facilitate identification of individuals wandering from their burrows. Certain aspects of the behaviour of H. cordiformis and the frequency of recording data for individuals reduced the possibility of 'mistaken identity.' The majority of behaviours occurred near the owner's burrow or involved frequent trips back to the burrows (e.g. feeding, maintenance and defense of burrows and forming mud balls). Six to 10 crabs were scanned continuously (in a clockwise direction around the site) allowing no more than a 3-minute gap between consecutive observations, and usually no more than 2 minutes. Because most of the behaviours were continuous and consecutive scans usually 'caught' each individual in the same behaviour as before (and usually in the same location), this also facilitated identification. The identification of each crab by sex, size, colour of chelae, location of burrow and other features adequately prevented confusion in all but 3-4 observations throughout the study. In these instances, the error was discovered later during the observational period when the misidentified crab entered its original burrow unchallenged and was either carrying a mud ball or proceeded to maintain the burrow, behaviours exhibited only by owners of burrows. In addition to recording behaviours, the position of the crab relative to its burrow (i.e. approximate distance and direction) was noted.

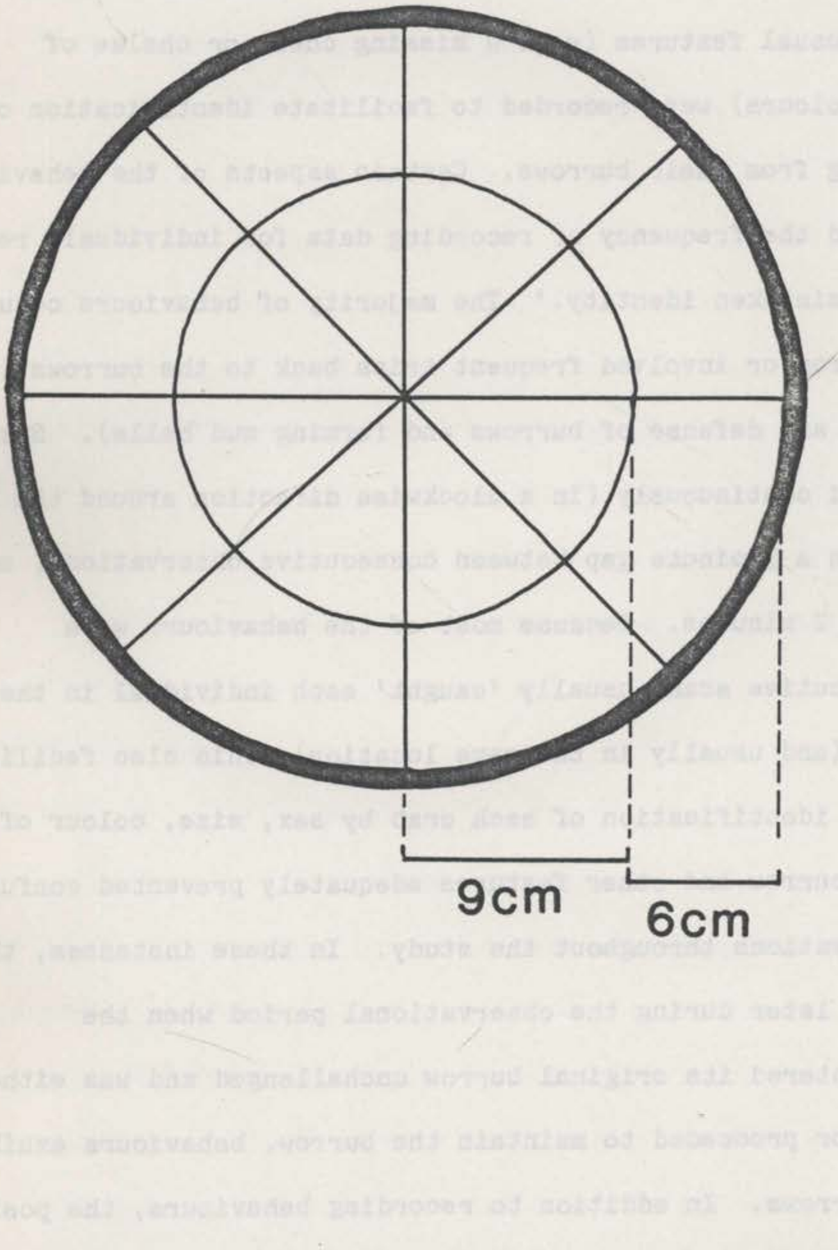

Figure 7.2. Circular grid to measure distances and positions of crabs relative to the burrow (for videotapes).

Data were recorded and analysed only for crabs owning burrows within the site. The behaviour of crabs that wandered through the site was recorded only when it elicited responses from a resident.

Videotaping involved all the above steps except that the behaviours were simultaneously recorded on videotape. The accompanying direct observations on paper were kept as 'back-up' copies and to provide data if crabs moved outside the range of the camera. The Sony video system included a DXC-1610P colour video camera mounted on a tripod and a portable VO-3800P video-cassette recorder, operated with a rechargeable battery lasting 40-45 minutes. An auxiliary battery pack provided an additional 40-45 minutes of operation. This equipment was set up beside me, also 1-1.5 m away from each study site. Recording was commenced after the emergence of the second crab to improve the probability of obtaining at least two 20-minute records for the 'sampling unit.' Because of limitations of the automatic exposure (aperture) control, which would not 'cope' with shadows falling across the study sites, video-recording was limited to the landward zone where shadows from mangrove trees were generally not a problem.

The last 60 seconds of each videotape were used to record placement of a circular grid, centered, in turn, over each burrow. The grid had a radius of 15 cm and was divided into 8 equal sectors (Figure 7.2). Each sector was divided into a central portion (radius = 9 cm) and a distal portion. Prior to reviewing videotapes on a television/monitor (to extract behavioural data), the grid was drawn onto the screen to provide an accurate (i.e. parallax-free) scale to measure distances and directions of crabs relative to their burrow. (Distortion by parallax was unavoidable because the camera could not be operated in a completely vertical position above each site due to limitations of the camera and tripod.)

During review of videotapes, the behaviours and positions of crabs were recorded using an event-recorder programme for a Commodore 4032 computer. Individual keys on the keyboard corresponded to behaviours, and a bell sounding every 15 seconds signalled the entry of data relating to the position of the crab within or beyond the circular grid. Review was limited to one crab at a time.

The primary advantage of the videotaping method was that it provided a continuous record of all behaviours and locations of crabs, except on the infrequent occasion when a crab wandered outside the field of view. Behaviours of short duration (e.g. a single wave, a lunge toward or away from another crab, or a sudden disappearance down a burrow) would not be overlooked as easily as by direct observation, which might miss as much as 3 minutes between consecutive observations on a given crab. For behaviours of longer duration (e.g. feeding, maintenance of burrows, courtship), both methods were expected to yield similar results. This prediction was tested for four categories of continuous behaviours (feeding, maintenance of burrows, pausing and 'other') and indicated no significant difference between methods (Appendices 7.1 and 7.2). Also, these analyses indicated no significant interactions of Method with any other factor; therefore, results of comparisons of the prevalence of behaviours among periods, days or sampling units would not be affected by using data recorded by either method (but see the description of occasional significant differences among Days, later in this section).

For direct observations, a 'sampling unit' consisted of observing a site for 20-30 minutes; each site contained at least six open burrows. For videotaping, sampling units were 18-20 minutes (= length of tapes); again each unit contained at least six open burrows. A maximum of eight sampling units using direct observation or four using videotapes could be obtained on any given day.

2. Assessment of temporal and spatial patterns of behaviour

To test the importance of time of day and tidal phase on behaviour, the sampling programme included observations during daylight and from post-emersion to pre-submergence. Because very few *H. cordiformis* were active on the surface at night (see Section A, this chapter), behavioural observations were made only from dawn until dusk. Unlike the pattern of emergence in Spring 1985, when crabs began to emerge within 30 minutes of emersion, in Autumn 1986 few crabs were active on the surface until 1000-1030, although the substratum might have already been emersed for several hours (Appendix 7.3). Nakasone (1982) noted a similar lag in emergence of *Uca vocans* during the colder months of the year. In addition, in Autumn, *H. cordiformis* went down and plugged their burrows at least one hour before submergence or by 1600-1630, although in Spring many crabs remained active on the surface until the incoming tide had surrounded the mounds they were on or until 1-2 hours after dusk. For these reasons, sampling and analyses of rhythmicity of behaviour were not done relative to time of day and tidal phase *per se* (i.e., post-emersion, mid-low tide, and pre-submergence), but instead relative to period of activity.

Three periods were used for observations and analyses: early, middle and late. The onset of the early period of activity was determined as that time when, on average, at least one open burrow could be found per 0.25 m^2 quadrat, tossed haphazardly ten times. The early period consisted of activities recorded during the first 2-2.5 hrs after the onset of activity on the surface, as determined above. The late period encompassed the last 2-2.5 hrs of activity before crabs began plugging their burrows to such an extent that fewer than one open burrow per quadrat could be found. The middle period varied in duration, depending on the extent of diurnal low tides, but commenced at least 30 minutes after the end of the early period and before the start of the late period.

Because of temporal limitations, observations of sampling units could not be replicated for each combination of Zone and Period on any given day. Testing of Day as a nuisance factor in preliminary analyses of behaviour indicated significant differences among days but no significant differences among sampling units on a given day (Appendices 7.1, 7.2, 7.4 and 7.5). Subsequent analyses of behaviour, therefore, incorporated sampling units from the same set of days for main factors being tested (e.g. Zone, Period, Sex, etc.).

In analyses comparing the proportion of time spent in various activities or at certain distances from the burrow, utilising data for more than one category of behaviour per crab would have resulted in non-independence among data. A crab spending most of its time feeding, for example, would have less time to maintain its burrow, form mud balls, etc. This problem was obviated by randomly selecting crabs for each behaviour separately, with the single

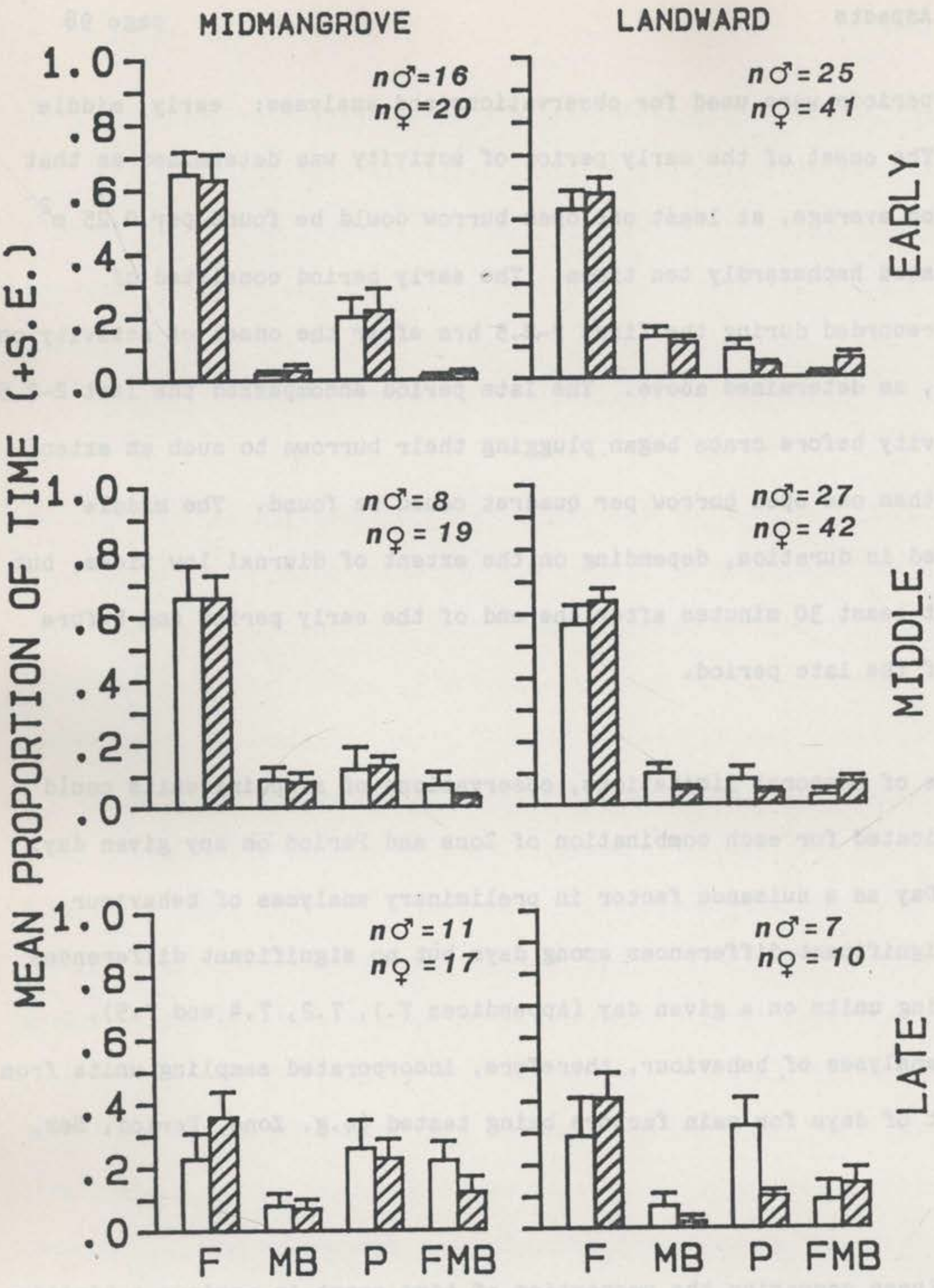

Figure 7.3. Mean proportion of time (+ S.E.) spent in the four most common behaviours. F = feeding, MB = maintaining burrows, P = pausing, FMB = forming mud balls. □ = males; ▨ = females. All sampling units within a given zone and period have been pooled.

restriction that data for different behaviours be from different crabs. The requirement of such independent samples plus restrictions imposed by the significance of Day (as a nuisance variable) frequently limited samples sizes to 2-5 crabs.

Results

1. Prevalence and Timing of Activities

The most prevalent behaviour observed for both sexes of *H. cordiformis* was feeding (Figure 7.3). During the early and middle periods of activity, crabs in the midmangrove and landward zones fed for at least 50% of the time they were observed. The remainder of the time was spent primarily on maintenance of the burrow, forming mud balls to take down the burrow and pausing (usually at the burrow). The proportion of time spent among these other common behaviours was fairly similar during the middle period of activity in each zone and during the early period of activity in the landward zone. During the early period in the midmangrove zone, however, pausing was approximately four times more prevalent than either maintaining burrows or forming mud balls. During the last two hours of activity on the surface, crabs spent less time feeding and more time pausing and forming mud balls than earlier in the day.

In each zone, feeding was significantly more prevalent than maintenance of burrows (Table 7.7). The proportions of time spent pausing and forming mud balls did not differ significantly in two of three analyses. In the analysis that indicated a significant difference, crabs spent more time pausing than forming mud balls. Period of activity, Zone and Sex had no

Table 7.7. Summary of analyses of variance of the proportion of time crabs spent in the four most common behaviours. If necessary, data were transformed to reduce heteogeneity of variances below a critical level of $P = 0.05$ for Cochran's test. Sexes were pooled for analyses not testing this factor. F.M.B. = forming mud balls.

	LEVELS OF FACTORS			DATES OF	
FACTORS TESTED	ZONE(S)	PERIOD(S)	BEHAV'S.	SAMPLING	SIGNIFICANT FACTORS AND ASSOCIATED MEANS (+ S.E.)
A. Period,Behav.	Midmang.	Early Middle Late	Feeding Maint.	31 May 86	Behav. F = 11.38 1,12 df $P < 0.01$ Feeding > Maint. 0.54 0.09 (0.22) (0.01)
B. Period,Behav.	Landward	Early Middle Late	Feeding Maint.	21 May & 2 June 86	Behav. F = 14.80 1,18 df $P < 0.005$ Feeding > Maint. 0.46 0.11 (0.09) (0.08)
C. Period,Behav.	Midmang.	Early Middle Late	Pausing F.M.B.	31 May 86	No significant factors (Residual df = 12)
D. Period,Behav.	Landward	Early Middle Late	Pausing F.M.B.	21 May & 2 June 86	No significant factors (Residual df = 18)
E. Zone,Sex,Behav.	Midmang. Landward	Early	Feeding Maint.	23-25 May 86	Behav. F = 65.00 1,16 df $P < 0.001$ Feeding > Maint. 0.66 0.002 (0.15) (0.002)
F. Zone,Sex,Behav.	Midmang. Landward	Early	Pausing F.M.B.	23-25 May 86	Behav. F = 13.40 1,16 df $P < 0.005$ Pausing > F.M.B. 0.21 0.02 (0.05) (0.02)

significant effects on the proportions of time spent in these four behaviours (Table 7.7; Figure 7.3).

The remaining activities comprising the behavioural repertoire of H. cordiformis were infrequent events, accounting for at most 5% of the time spent on the surface (e.g. courtship/coupling, waving displays, combat, etc.). These behaviours were observed in both zones and during all three periods of activity. (A summary of the frequency and nature of these events is given in Appendix 7.6.)

The last behaviour a crab engages in before ending its period of activity on the surface is plugging its burrow; therefore, this behaviour always occurred during the late period of activity for that individual. During the 5-week sampling period, only 1-2 crabs plugged their burrows before the late period (as determined for the population on that day, for that zone). The end of the period of activity on the surface was, therefore, strongly synchronised for the population as a whole.

The final category accounting for the remainder of time crabs were observed in the sampling programme was time spent by crabs in the burrow after initial emergence. Many crabs spent little or no time in burrows, and a few crabs spent 30-70% of the time underground. This resulted in skewness of observations (Figure 7.4) which was reduced by transforming the data to arcsin $\sqrt{x}$ in analyses of variance. There was no significant effect of Zone, but Sex and Period were significant in several analyses (Table 7.8; Appendix 7.7). When differences did occur, they were inconsistent between dates of sampling and often interacted with other factors.

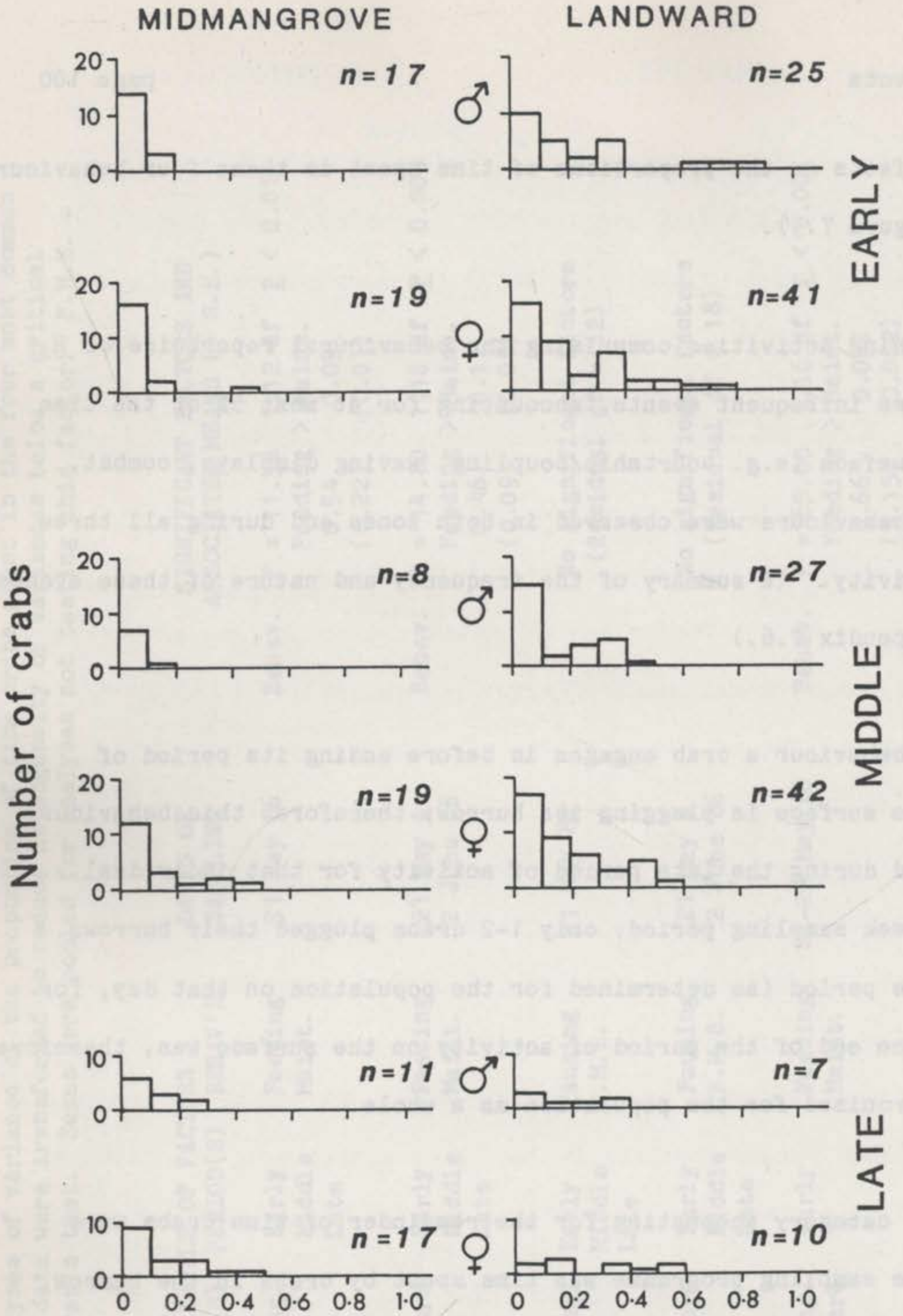

Figure 7.4. Frequency distribution of the numbers of crabs spending various proportions of time inside the burrow.

Table 7.8. Summary of analyses of variance of the proportion of time crabs spent in burrows. Because of skewness of data and/or heterogeneity of variances, data were transformed to arcsin $\sqrt{x}$. For each analysis, Cochran's test was not significant ($P > 0.05$). Sexes were pooled for analyses not testing this factor. Means in table are untransformed.

FACTORS TESTED	LEVELS OF FACTORS ZONE(S)	PERIOD(S)	DATES OF SAMPLING	SIGNIFICANT FACTORS AND ASSOCIATED MEANS (+ S.E.)
A. Zone, Sex, Period	Midmang. Landward	Early Middle	24 May 86	No significant factors (Residual df = 8)
B. Zone, Sex, Period	Midmang. Landward	Early Middle	23-24 May 86	Period F = 4.83 1,16 df $P < 0.05$ Early < Middle 0.01 0.05 (0.01) (0.02)
C. Sex	Midmang.	Late	18 May 86	Sex F = 15.00 1,10 df $P < 0.005$ Male < Female 0.03 0.17 (0.02) (0.03)
D. Sex, Period	Landward	Early Middle Late	2 June 86	S x P F = 5.65 2,6 df $P < 0.05$ (see Appendix 7.7 for means)
E. Zone, Period	Midmang. Landward	Early Middle	23-24 May 86	Period F = 7.00 1,40 df $P < 0.025$ Early < Middle 0.02 0.10 (0.01) (0.04)
F. Period	Midmang.	Early Middle Late	31 May 86	No significant factors (Residual df = 15)
G. Period	Landward	Early Middle Late	2 June 86	No significant factors (Residual df = 21)

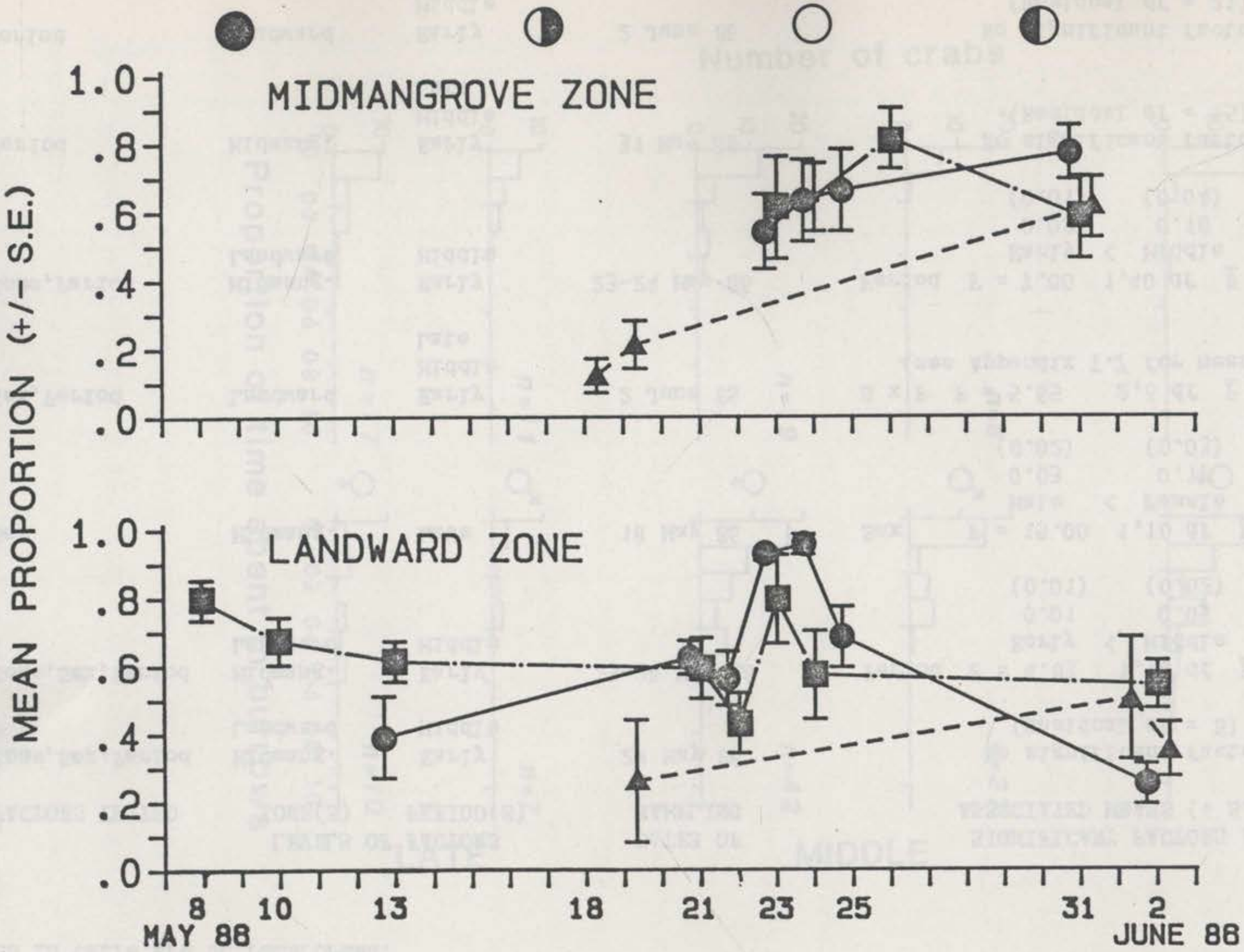

Figure 7.5. Mean proportion of time (+/- S.E.) spent feeding relative to the lunar phases during the sampling period from May to June 1986. Males and females have been pooled. Sample sizes as in Figure 7.3. Circles = early, squares = middle, and triangles = late period of activity.

Rigorous examination of the potential correlation between lunar phases and behaviour could not be done because the 5-week sampling programme did not allow replication of observations for each lunar phase. Plots of proportion of time spent in six behaviours or in burrows versus lunar phase suggest, at first glance, that some activities suddenly increase or decrease near a full moon (e.g. Feeding, Figure 7.5). These trends could be artificial, however, because sampling was done on a 6-day run of consecutive days around the time of full moon and the remainder of sampling was more spread out. The 5- and 6-day gaps in sampling around the phases of quarter moons could have missed similar peaks and troughs in behaviour. The suggestion of a semilunar pattern in these data merits a longer-term study incorporating several months of observation to allow replication of observations among lunar phases, and subsequent statistical analyses.

For crabs leaving the burrow at least once, the mean numbers of excursions per crab (per sampling unit) were similar in all 3 periods of activity, between sexes and between zones (Table 7.9). Similarly, analyses of the proportions of crabs leaving burrows for at least one excursion indicated no significant effects of Sex, Zone or Period (Table 7.10.; Appendix 7.8). In these analyses, data from the late period could not be used because sample sizes were too small on the two days (31 May and 2 June 1986) when all three periods were sampled on the same day.

There were no significant effects of Sex or Period on the mean duration of completed excursions (i.e. those terminating at the burrow before the end of the 20-minute sampling period; ANOVA, $\underline{P} > 0.25$ for Period, Sex and P x S;

Table 7.9. Analysis of variance of the mean number of excursions per crab (per sampling unit) for males and females.

A. Analysis of effects of Period and Sex. Data were collected during the early and middle periods of activity on 6 days in May and June 1986. Data were untransformed, and Cochran's test was not significant ($\underline{P} > 0.05$); $\underline{n} = 6$ sampling units.

SOURCE	DF	MS	F	P
Period	1	0.004	0.02	> 0.50
Sex	1	0.43	1.95	> 0.10
P x S	1	0.02	0.09	> 0.50
Residual	20	0.22		

B. Analysis of effects of Zone and Sex. Data were collected from each tidal zone, during the early period of activity on 23, 24 and 25 May 1986. Data were untransformed, and Cochran's test was not significant ($\underline{P} > 0.05$); $\underline{n} = 3$ sampling units.

SOURCE	DF	MS	F	P
Zone	1	0.15	0.71	> 0.25
Sex	1	0.03	0.14	> 0.50
Z x S	1	0.24	1.14	> 0.25
Residual	8	0.21		

C. Mean number of excursions per crab (+ S.E.) for crabs leaving the burrow at least once during the period of observation. $\underline{m}$ = number of sampling units; $\underline{n}$ = number of crabs.

Males ($\underline{m} = 39$, $\underline{n} = 82$)	1.47 (0.29)
Females ($\underline{m} = 39$, $\underline{n} = 119$)	1.42 (0.15)
Early Period ($\underline{m} = 32$, $\underline{n} = 84$)	1.52 (0.25)
Middle Period ($\underline{m} = 33$, $\underline{n} = 93$)	1.51 (0.17)
Late Period ($\underline{m} = 13$, $\underline{n} = 24$)	1.31 (0.27)
Midmangrove Zone ($\underline{m} = 28$, $\underline{n} = 64$)	1.34 (0.21)
Landward Zone ($\underline{m} = 50$, $\underline{n} = 137$)	1.56 (0.21)

Table 7.10. Analyses of variance of the proportion of males and females leaving the burrow for at least one excursion. Means associated with these analyses are in Appendix 7.8.

A. Analysis of effects of Period and Sex. Data were collected during the early and middle periods of activity on 6 days in May and June 1986. Data were untransformed, and Cochran's test was not significant ($P > 0.05$); $n = 6$ sampling units.

SOURCE	DF	MS	F	P
Period	1	0.02	1.00	> 0.25
Sex	1	0.01	0.50	> 0.25
P x S	1	0.03	1.50	> 0.10
Residual	20	0.02		

B. Analysis of effects of Zone and Sex. Data were collected during the early period of activity on 23, 24 and 25 May 1986, from each tidal zone. Significant heterogeneity of variances was unresolvable by transformation of data (Cochran's test, $P < 0.01$), therefore, only non-significant results in the ANOVA are reliable (nb: heterogeneity resulted from three means with 0 variance and one mean with a variance of 0.07; see Appendix 7.8). $n = 3$ sampling units.

SOURCE	DF	MS	F	P
Zone	1	0.03	1.50	> 0.25
Sex	1	0.03	1.50	> 0.25
Z x S	1	0.03	1.50	> 0.25
Residual	8	0.02		

C. Mean proportion of crabs per sampling unit (+ S.E.) leaving the burrow for at least one excursion during the period of observation. m = number of sampling units; n = number of crabs.

Males ($m = 42$, $n = 95$)	0.82 (0.13)
Females ($m = 43$, $n = 148$)	0.67 (0.12)
Early Period ($m = 34$, $n = 102$)	0.80 (0.11)
Middle Period ($m = 33$, n 96)	0.89 (0.06)
Late Period ($m = 18$, $n = 45$)	0.53 (0.19)
Midmangrove Zone ($m = 31$, $n = 91$)	0.70 (0.13)
Landward Zone ($m = 54$, $n = 152$)	0.78 (0.17)

1,8 df). The mean numbers of minutes per excursion (+ S.E.) were

Early Period:	
Males (6 crabs, 9 excursions)	4.97 (1.32)
Females (10 crabs, 20 excursions)	3.67 (0.49)
Middle Period:	
Males (16 crabs, 19 excursions)	5.55 (0.84)
Females (20 crabs, 34 excursions)	4.17 (0.56)

Only data from videotapes were analysed because quick returns to the burrow followed immediately by another excursion might have been more easily missed during direct observation. Because videotaping was not used during the late period or in the midmangrove zone, this period and zone could not be included in statistical analyses.

Most crabs making at least one trip from the burrow returned to the burrow at least once during the period of observation. The mean number of returns per crab was

Early Period:	
Males (14 crabs)	0.68 (0.27)
Females (12 crabs)	1.07 (0.41)
Middle Period:	
Males (7 crabs)	1.04 (0.17)
Females (13 crabs)	0.71 (0.23)

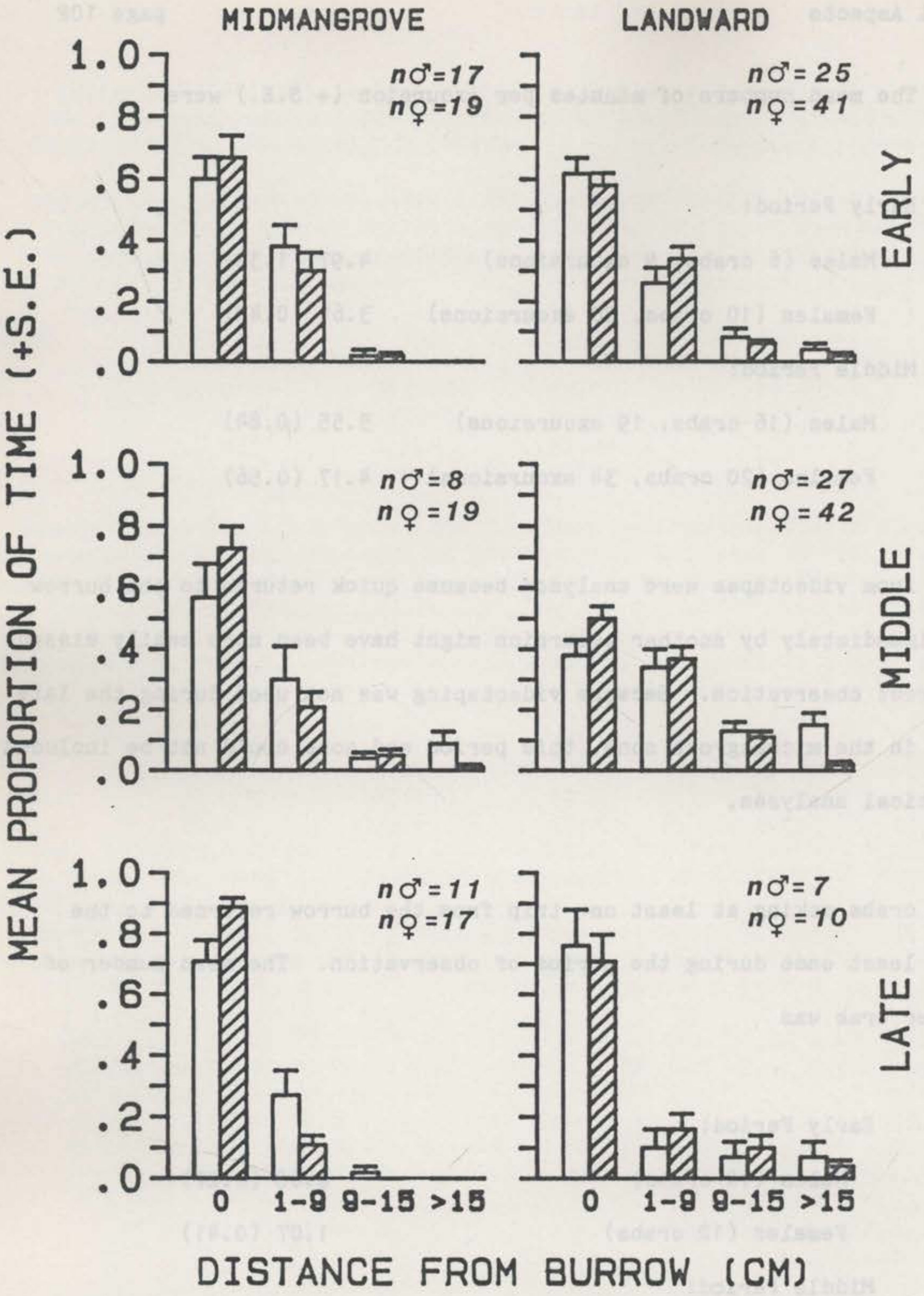

Figure 7.6. Mean proportion of time (+ S.E.) spent at or away from the burrow in each zone, during three periods of activity. ☐ = males; ▨ = females.

There was no significant difference between sexes nor between periods of activity (ANOVA, $\underline{P} > 0.10$; 1,20 df). For reasons discussed above, data from the late period and midmangrove zone could not be used. Examination of the prevalence of returns to the burrow indicated that the proportion of crabs returning to the burrow at least once during the sampling period did not differ between sexes or periods (ANOVA, $\underline{P} > 0.10$; 1,20 df). The mean proportions of crabs returning to the burrow at least once were

Early Period:	
Males (11 sampling units)	0.74 (0.12)
Females (11 sampling units)	0.89 (0.06)
Middle Period:	
Males (12 sampling units)	0.60 (0.14)
Females (12 sampling units)	0.98 (0.02)

2. Small-scale Spatial Patterns: Distances and Directions from Burrows

Crabs spent at least 70% of the time at or within 9 cm of the burrow (Figure 7.6). There were no obvious nor consistent differences between the sexes, except for a greater tendency for males rather than females to wander more than 15 cm from the burrow during the middle period of activity (in each zone).

Prior to analyses of the effects of Sex, Period and Zone on spatial patterns, the significance of the nuisance variables Method of recording, Day of sampling and Sampling Unit was tested. As in the previous analyses of temporal patterns, Method of recording and Sampling Units on a given day were

Table 7.11. Summary of analyses of variance of the proportion of time crabs spent at or 1-9 cm away from the burrow (Distance). For each analysis, data were untransformed, and Cochran's test was not significant ($P > 0.05$). Sexes were pooled for analyses not testing this factor.

FACTORS TESTED	LEVELS OF FACTORS		DATES OF SAMPLING	SIGNIFICANT FACTORS AND ASSOCIATED MEANS (+ S.E.)
	ZONE(S)	PERIOD(S)		
A. Sex, Period, Dist.	Midmang.	Early Middle	24 & 31 May 86	No significant factors (Residual df = 8)
B. Sex, Period, Dist.	Landward	Early Middle	7 days in May & June 86	Dist. F = 12.43 1,48 df $P < 0.005$ At burrow > 1-9 cm away 0.54 0.29 (0.11) (0.09)
C. Zone, Sex, Dist.	Midmang. Landward	Early	23-25 May 86	No significant factors (Residual df = 16)
D. Period, Dist.	Midmang.	Early Middle Late	31 May 86	Dist. F = 35.40 1,12 df $P < 0.001$ At burrow > 1-9 cm away 0.79 0.16 (0.15) (0.09)
E. Period, Dist.	Landward	Early Middle Late	2 June 86	Dist. F = 22.17 1,18 df $P < 0.001$ At burrow > 1-9 cm away 0.70 0.23 (0.13) (0.09)

not significant, but spatial patterns differed among Days (Appendices 7.9 - 7.11). Data for analyses of main factors, therefore, were used from the same day or same set of days.

The proportion of time spent at the burrow or 1-9 cm from the burrow were analysed to test if differences among periods of activity, between zones or between sexes were significant. The remaining two categories of distance, 9-15 cm and > 15 cm, contained too few data for statistical analyses. Period, Sex and Zone did not significantly affect the proportion of time crabs spent at or 1-9 cm away from the burrow (Table 7.11). Three of these five analyses, however, indicated that crabs spent significantly more time at than away from the burrow.

The maximal distance crabs moved from their burrows appeared to be greater for males than females during the middle period of activity in both zones and during the late period in the midmangrove zone (Figure 7.7). During the middle period, males in the midmangrove and landward zones traversed a mean maximum distance of 14.0 cm and 15.4 cm, respectively, whereas females went only 5.9 cm and 9.5 cm. During the late period in the midmangrove zone, crabs stayed much closer to the burrow, traversing a mean maximum distance of only 4.8 cm (for males) and 1.6 cm (for females). Although the data in Figure 7.7 (for the entire sampled population) suggest that Sex and Period might have interacted in their effects on maximum distances, statistical analyses supported this prediction for crabs in the landward zone only (Table 7.12, B). For crabs used in this analysis, males and females made excursions of similar maximum distance during the early period of activity (6.64 cm for males and 7.46 cm for females). During the

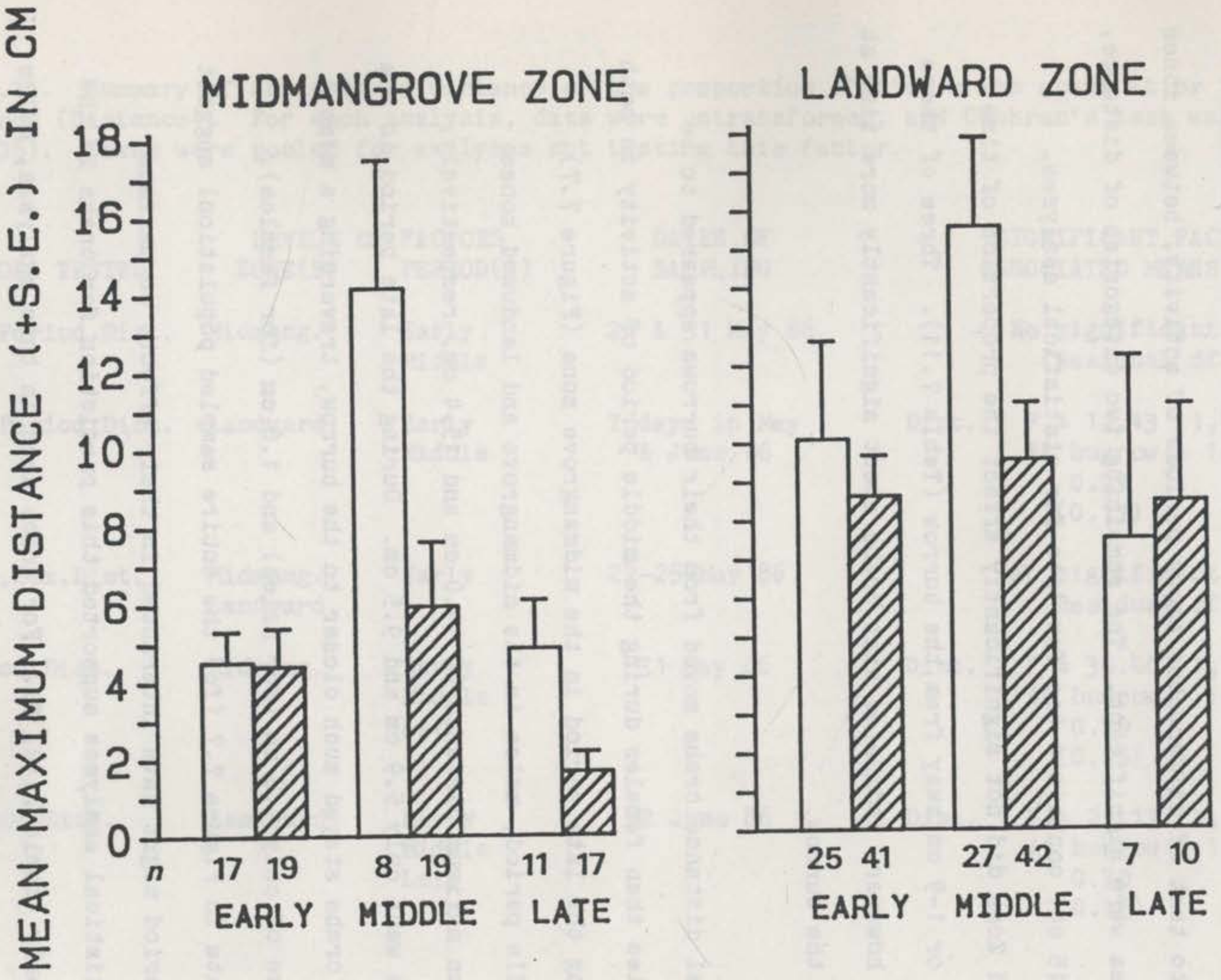

Figure 7.7. Mean maximum distance (+ S.E.) crabs moved from their burrows in both zones during three periods of activity. ☐ = males; ▨ = females.

Table 7.12. Summary of analyses of variance of the mean maximal and minimal distances traversed by crabs. If necessary, data were transformed to reduce heterogeneity of variances below a critical level of $P = 0.05$ for Cochran's test. Sexes were pooled for analyses not testing this factor. Means in table are untransformed; units = cm. F.M.B. = forming mud balls.

FACTORS TESTED (DATA)	LEVELS OF FACTORS ZONE(S)	PERIOD(S)	BEHAV'S.	DATES OF SAMPLING	SIGNIFICANT FACTORS AND SNK TESTS ($P = 0.01$)
A. Sex, Period (Max. Dist.)	Midmang.	Early Middle	All	24 & 31 May 86	No significant factors (Residual df = 16)
B. Sex, Period (Max. Dist.)	Landward	Early Middle	All	5 days in May & June 86	Period F = 5.52 1,40 df $P < 0.025$ S x P F = 5.62 1,40 df $P < 0.025$ (see text, pp. 104-105 for means)
C. Zone, Sex, Period (Max. Dist.)	Midmang. Landward	Early Middle	All	23-24 May 86	Z x P F = 9.04 1,16 df $P < 0.01$ (see text, p. 106 for means)
D. Zone, Sex, Behav. (Min. Dist.)	Midmang. Landward	Early Middle Late (Pooled)	Pausing Feeding F.M.B.	6 days in May & June 86	Behav. F = 70.78 2,84 df $P < 0.001$ Pausing = Feeding < F.M.B.[1] 0.31 0.91 12.56 (0.22) (0.31) (3.17)
E. Zone, Sex, Behav. (Max. Dist.)	Midmang. Landward	Early Middle Late (Pooled)	Pausing Feeding F.M.B.	6 days in May & June 86	Behav. F = 54.25 2,84 df $P < 0.001$ Pausing < Feeding < F.M.B.[1] 0.31 6.19 11.91 (0.22) (1.67) (1.67)

[1] Note: random selection of crabs for each analysis resulted in the mean minimum distance for forming mud balls being greater than the mean maximum distance for this behaviour.

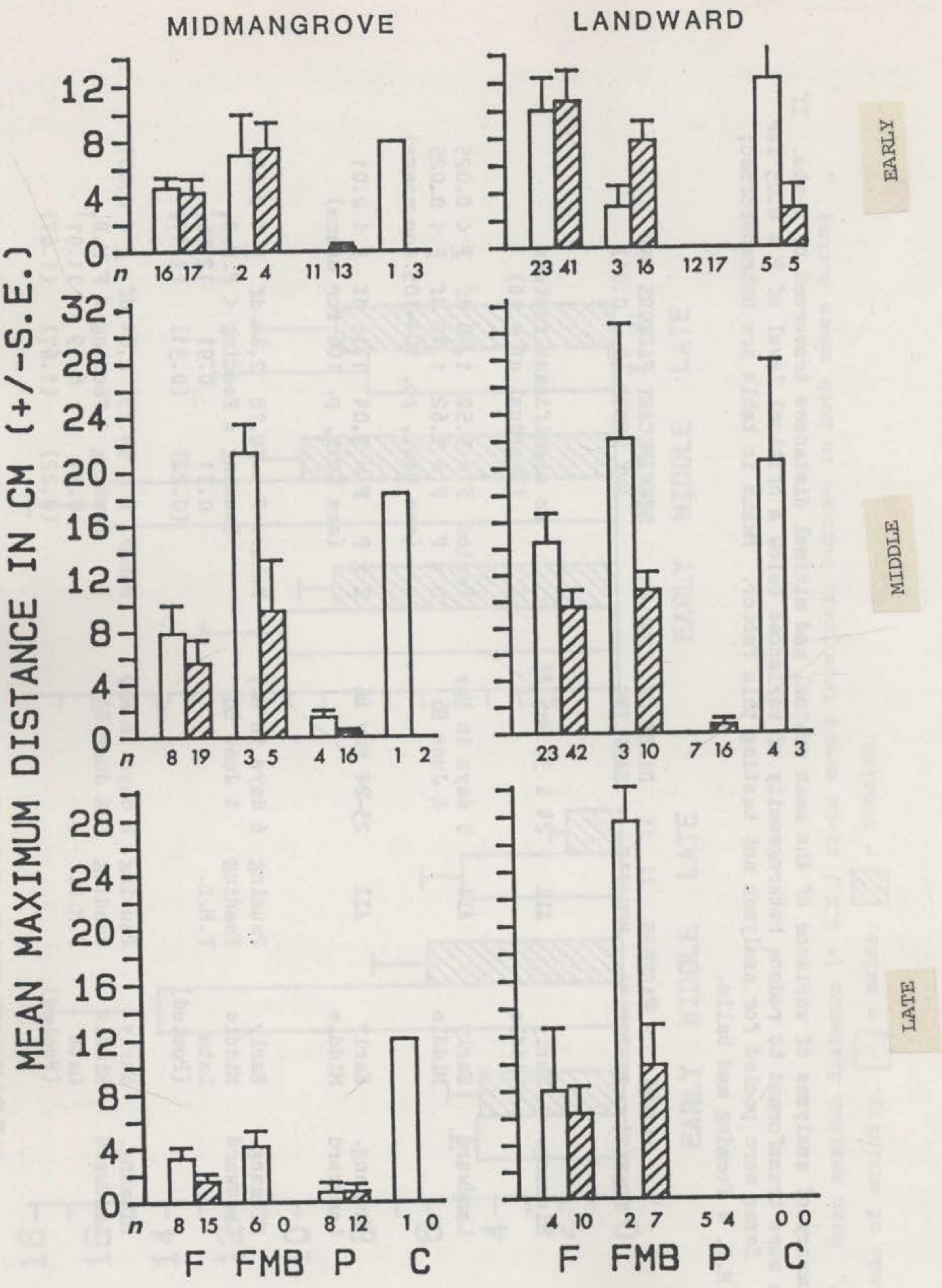

Figure 7.8. Mean maximum distance (+ S.E.) from burrows at which four activities were performed by crabs during three periods of activity. F = feeding, FMB = forming mud balls, P = pausing, and C = courting. □ = males; ▨ = females.

middle period of activity, however, males went significantly further than they did earlier (17.82 cm vs. 6.64 cm) whereas females did not show such a large increase. Data for the analysis of distances traversed in the midmangrove zone also suggested a large increase in distances traversed by males from the early to middle period of activity, whereas females showed a greater tendency to stay closer to the burrow during the middle period relative to the early period.

Two behaviours were probably most responsible for the striking increase in mean maximum distance for males during the middle period relative to the early period of activity: forming mud balls and courtship (Figure 7.8). In the midmangrove zone, the increase in the mean maximum distance from the early to middle period of activity was from 7.0 cm to 21.0 cm for forming mud balls, and from 8.0 cm to 20.0 cm for courting (although there was only one occurrence of courtship during each period). In the landward zone, a similar trend was observed: the maximum distance for forming mud balls increased from 3.0 cm to 21.8 cm, and, for courting, from 12.2 cm to 20.0 cm from the early to the middle period of activity. During the late period of activity, males in the midmangrove zone formed mud balls closer to the burrow than during the middle period (4.2 cm vs. 21.0 cm, for late vs. middle), but males in the landward zone showed an increase in the maximum distance at which this activity was performed (21.8 cm during the middle period vs. 27.8 cm during the late period). Unfortunately, sample sizes for several of these behaviours were very small (1-3 individuals), and statistical analyses could not be done.

When Zone was included in the analysis of effects of Period and Sex on the maximum distance traversed, Sex was shown to have no effect but Zone and Period interacted significantly (Table 7.12, C). During the early period of activity, crabs went further from their burrows in the landward zone than in the midmangrove zone (9.17 cm vs 2.67 cm, respectively, when sexes were pooled). During the middle period, however, the opposite pattern was observed: the mean maximum distances traversed were 4.67 cm in the landward zone and 12.50 cm in the midmangrove zone.

Another aspect of small-scale spatial patterns of movement was the relationship between certain prevalent behaviours and the distances at which these typically occurred. Analysis of the minimum distances at which crabs paused, fed and formed mud balls indicated that crabs fed and paused closer to their burrows than when they formed mud balls (Table 7.12, D). The mean minimum distances for each of these behaviours (when sexes were pooled) were 0.31 for pausing, 0.91 cm for feeding and 12.56 cm for forming mud balls. The analyses indicated no significant differences between males and females or between crabs in either zone.

A similar analysis of the maximum distances at which these activities were performed demonstrated that pausing was restricted closest to the burrow (mean = 0.31 cm away). Feeding could occur significantly further (mean = 6.19 cm), and forming mud balls could be done significantly further than feeding (mean = 11.91 cm; Table 7.12, E).

In summary, when crabs paused they were always at or very close to the burrow; they fed over a wide range of distances from the burrow; and, on

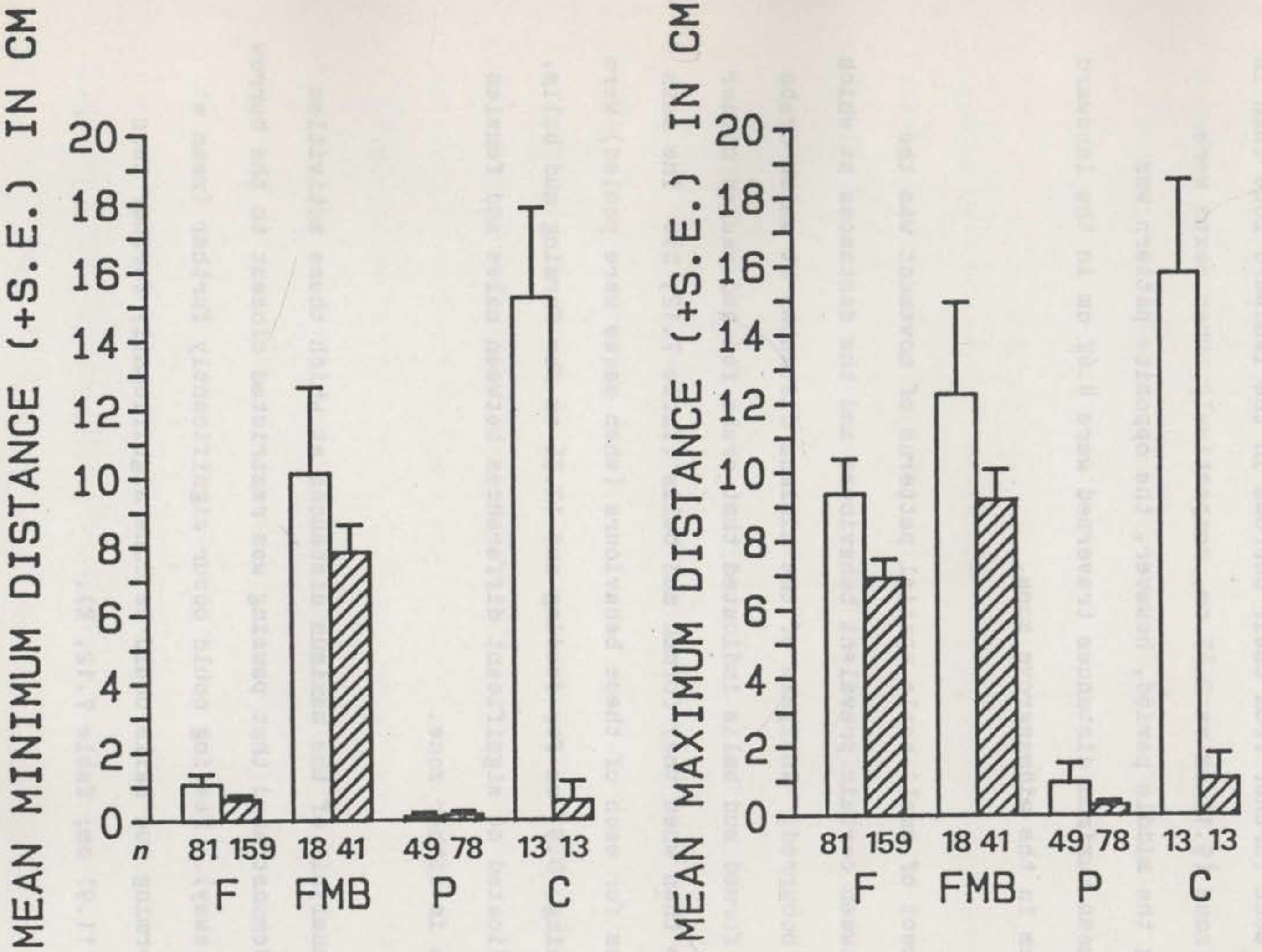

Figure 7.9. Mean minimal and maximal distances (+ S.E.) from burrows at which four behaviours were performed by crabs. Periods of activity, zones and days have been pooled. F = feeding, FMB = forming mud balls, P = pausing, and C = courting. □ = males; ▨ = females.

average, they formed mud balls only at some distance from the burrow. When crabs collected a clod of mud to plug the burrow at the end of the period of activity, they frequently took material from just outside the burrow. When forming mud balls to bring into the burrow, however, crabs collected material just outside the burrow on only 6 of 74 occurrences of this behaviour. As in the previous analysis, there were no significant effects of Zone or Sex.

There was a large difference between the sexes in the mean distances from the burrow at which courtship occurred: 15.23-15.77 cm for males and 0.57-1.08 cm for females (Figure 7.9). This difference was not surprising, because male H. cordiformis always courted females at or just outside a female's burrow. Because this pattern is well-known for this species (Griffin 1968), further analyses were unnecessary.

The final aspect of the examination of small-scale spatial patterns was to test whether crabs making multiple excursions from the burrow did so over the same or different sectors of substratum surrounding the burrow. Because crabs spend at least 50% of the time processing sediment (either by feeding or forming mud balls), it was thought that they might avoid previously visited patches of substratum from which diatoms and other food had been extracted. An alternative possibility was that crabs might favour using one sector repeatedly because familiarity with a given path might make navigation back to the burrow easier should some threatening situation arise and a crab have to react quickly (e.g. arrival of a predatory bird or wandering crab). Analysis of directonal data compared observed and expected frequencies (if directions were random) of visits to one of eight 45 degree sectors of substratum surrounding burrows of crabs making at least 3 excursions, using the method described by Underwood (1978). The directions crabs moved from their burrows were not significantly different from random ($\underline{P} > 0.10$, 25 df).

Discussion

Not surprisingly, crabs were found to spend more time on activities necessary for survival (e.g. feeding and maintenance of burrows) than in other behaviours which are not as necessary in the short run (e.g. courtship and defence of burrows). These latter activities probably are more prevalent during the warmer months of the year, when H. cordiformis are actively breeding. Unfortunately, this study was done during the last month of activity on the surface before the population hibernates (late June to late August, for the 3.5 years that local populations were examined). Because of this, crabs were in general less active than at other times of the year and might, therefore, have been spending less time in activities not directly related to daily survival.

Although Griffin (1968) reported that during winter crabs emerge onto the surface to feed every few days, virtually no crabs were ever seen on the surface during the three winters I sampled crabs in swamps near Sydney. Local populations might spend a greater proportion of their time in Autumn feeding and maintaining burrows because during winter there is little or no opportunity for them to do these activities. Crabs probably survive without emerging onto the surface by feeding on the material in their burrow, living off reserves of fat or maintaining a slow rate of metabolism. If the second mechanism is important for survival over winter, then time apportioned for feeding might, in fact, be emphasised in late autumn at the expense of other activities.

Most analyses in this study indicated no significant differences between males and females. Because all crabs must feed, maintain their burrows, and perform other basic 'maintenance' activities, differences between the sexes would not be expected for these behaviours. If the sexes differ in their behaviour, the differences should be more obvious in reproductive activities than in these maintenance activities.

Griffin (1968) and I have found that only males initiated courtship. Courtship involves a male approaching a female at her burrow and might, therefore, have led to a greater number of excursions (or excursions of longer duration) from the burrow by males than by females. Analyses, however, indicated no significant differences between the sexes. Griffin (1968) also found that most fighting (displays and combat) occurred between males whereas females in the present study were frequently involved in displays and combat. If local populations of H. cordiformis have a peak season for such agonistic interactions, sexual differences might manifest themselves at that time.

In general, behaviour did not differ in any consistent manner between crabs in the midmangrove and landward zones. Zones were sampled separately because differences in the nature of the substratum, duration of emersion or some other factor might have led to differences in behaviour. The greater duration of emersion in the landward zone, for example, might have enabled crabs there to spend a greater proportion of time engaged in activities not directly related to survival than crabs in the midmangrove zone. Also, crabs are, in general, larger and the sex ratio is skewed toward more females in the landward zone relative to the midmangrove zone (Chapter 4) and these differences might affect the prevalence of courtship or other behaviours. The behaviour of several species of fiddler crabs differs among zones because males inhabit special areas for courtship that are typically landward of the population of females and non-reproductive males (Crane 1975; Hyatt 1977; Hyatt and Salmon 1978; Salmon 1983). Neither male nor female H. cordiformis inhabited distinct areas for courtship nor did they show any difference in the proportion of time spent courting or in other intraspecific interactions.

A surprising result of the behavioural analyses in this study was the lack of a significant difference among periods of activity in the proportion of time spent in various activities nor the proportion of crabs involved in these activities. With the exception of plugging burrows (which must occur at the end of a crab's period of activity), H. cordiformis did not systematically proceed from one phase of activity to another from the early to late period of emersion. Casual observations by Griffin (1968) suggested the following sequence of activities for H. cordiformis: feeding for an hour or more after emergence, then displaying and/or wandering, with the formation of mud balls at the end of the period of activity. He did note some variability in this pattern on any given day (e.g. some crabs displayed until the rising tide almost reached their burrows) and variability among days (e.g. on some days most crabs were maintaining burrows and on other days displaying). Results of the present study, however, indicate that the suggestion of any set sequence would be misleading.

A longer-term sampling programme would enable examination of the importance of lunar phases with respect to behaviour. The majority of examples of semilunar rhythmicity in crabs involve reproductive behaviours (e.g. hatching of larvae, Christy 1978 and Salmon et al. 1986; and construction of burrows for courtship, Zucker 1974). Sampling in the present study encompassed only one complete lunar cycle, and reproductive activities were rare events during this period; therefore, the likelihood of detecting such effects were small.

Another behaviour that might have been under-represented in this study was wandering of 'large numbers' (unspecified) of larger males without returning to the same burrow (Griffin 1968). This behaviour occurs in all tropical species of fiddler crabs and in some temperate species (Crane 1975). Nakasone (1982), however, noted that Uca vocans only formed herds from late spring to early autumn; the absence of herding in H. cordiformis might have been related to sampling so close to winter. At least 50% of the crabs leaving a burrow returned to the burrow within the 20-minute period of observation, and in most cases (8 of 12 combinations of Sex, Period and Zone) at least 85% returned at least once. These means are minimal estimates because crabs not returning to their burrow by the end of the period of observation might have returned later. Estimates of the proportion of crabs simultaneously involved in such behaviour have not been reported for semaphore crabs; however, Nakasone (1982) observed 10 of 12 crabs in one quadrat become wanderers during the 4 hours he watched a 5 m^2 site. Crane (1975) defined two types of wandering: i) non-aggressive wandering, wherein a male moves to the seaward edge of mangrove swamps or salt marshes to feed and does not threaten or enter into combat, nor court, and ii) aggressive wandering, wherein a male moves at random through a population, engaging in combat and courtship. Neither type of behaviour was observed in this study.

Sampling at other times of the year would be necessary to determine whether wandering ever occurs in local populations.

Griffin (1968) pointed out that the courtship display of H. cordiformis (vertical, partially unflexed waving) resembled that of the less advanced species of fiddler crabs, those with a narrow front (i.e. the middle section of the anterior carapace that projects forward and down between the orbits; Crane 1975). Although waving was not observed in this study, other aspects of pre-copulatory behaviour which were observed are similar to those of the narrow-fronted fiddler crabs. These included the observations that i) males approach females at their burrows, with or without waving; ii) copulation (coupling) is usually preceded by stroking of the female's carapace by the male's walking legs and/or picking at the female's carapace or legs by the male's cheliped; and iii) copulation occurs on the surface of the substratum.

Male and female H. cordiformis spent most of their time at or very near the burrow. Maintaining such a close proximity would make burrows easier to defend (should a non-burrow-owning wanderer approach) and might also advertise ownership, thus discouraging some attemps at taking over another's burrow. This sort of advertisement was described by Griffin (1968) as the primary function of pausing behaviour, because crabs engaged in this activity were never challenged by another crab. Results of the present study support this proposed function in that crabs paused only when at or within 1-2 cm of the burrow. Crabs, therefore, leave the burrow to engage in some activity (e.g. courtship, feeding, and forming mud balls) but return to the burrow and remain there between such bouts of behaviour.

Two activities which involve the collection and/or processing of sediment are feeding and forming mud balls (to take down the burrow). Both activities should decrease the availability of food (diatoms and other algae, detritus, etc.) in the substratum. Crabs fed at the entrance to the burrow and also over a wide range of distances from the burrow but nearly always collected material to bring down the burrow from some distance away (15-16 cm from the burrow, on average, Figure 7.9). Analyses of the mean maximum distances at which crabs fed and formed mud balls indicated that the latter occurred significantly further from the burrow than the former. Because crabs fed closer to the burrow and spent much more time feeding than forming mud balls during the early and middle periods of activity (Figure 7.3), the abundance of food might have been greatly reduced within the first 5-10 cm of the burrow relative to the abundance of food beyond this range. Sediment collected beyond this range would, therefore, probably have a greater concentration of food. Field and laboratory studies by Robertson et al. (1980) demonstrated that Uca pugilator could respond to differences in the concentration of food on a scale of millimetres (by probing the substratum with the chelae), and crabs foraged less frequently in patches with small concentrations of food relative to adjacent areas with greater concentrations. If H. cordiformis can also detect differences in availability of food and food is more abundant further from the burrow, this model might explain why this species forms mud balls further from the burrow than the typical distances at which it feeds.

During low tide, a patch of substratum with little food could be rejected in favour of 'greener pastures' elsewhere. During periods of submergence, however, crabs are restricted to their burrows and to the supply of food (in the form of mud balls) collected from above during the previous low tide. An argument against this model is that the feeding activities of neighbouring crabs might deplete the abundance of food at some distance from another crab's burrow. A gradient of increasing availability of food further from one crab's burrow and resulting from the activities of that crab might be greatly affected (even obliterated) by the net effect of all neighbouring crabs behaving in a similar manner. The proposed model could be tested by measuring the effects of crabs singly and in natural aggregations on the distribution and abundance of food relative to the burrow. Determining the spatial distribution of nearest neighbours would also indicate how likely the feeding activities of one crab might influence the availability of food within the foraging area of another crab.

Finally, if the distance at which H. cordiformis form mud balls is a matter of choice (as opposed to an inherent tendency to form mud balls at a greater distance from the burrow than that used for feeding), then the ability of this species to detect food availability could be determined using methods similar to those of Robertson et al. (1980), and subsequent experiments could be done to determine if, indeed, H. cordiformis prefer to form mud balls from substratum having greater concentrations of food.

Although most analyses of the proportion of time spent at various distances from the burrow or engaged in the four most common behaviours indicated no significant effect of Sex, Zone or Period, these factors did have a significant effect on the maximum distance crabs wandered from their burrows (Table 7.12). Males fed, formed mud balls and engaged in courtship further from their burrows than females. The most striking difference was in the mean maximum distance at which each sex was involved in this third behaviour (because males courted females at their burrows). A significant effect of period of activity indicated, in several analyses, that males wandered further from their burrows during the middle period of activity than during the early period (Table 7.12, B). The behaviour associated with the greatest increase in mean maximum distance from the early to the middle period of activity was forming mud balls (Figure 7.8). If crabs are removing food from close to the burrow (by feeding and forming mud balls) during the early period, then they might be expected to engage in both of these activities further from the burrow as time progresses. The mean maximum distance for feeding, however, did not increase. Perhaps (for reasons explained earlier) a large concentration of food is more important in the formation of mud balls than for feeding and, therefore, crabs collected substratum for mud balls in less-heavily foraged sediments (further from the burrow). If collecting nutrient-rich substratum is a real concern for H. cordiformis, then the lack of a similar tendency in females is enigmatic. The maximum distance at which courtship occurred also increased from the early to the middle period in each zone. This might have contributed somewhat to the overall increase (i.e. pooled for all behaviours) in distances males traversed during the middle period (and led to the significant Period x Sex interaction in the analysis presented in Table 7.12, B).

Finally, with the exception of males forming mud balls (in the landward zone), all other behaviours were done closer to the burrow during the late period than during the middle period (Figure 7.8). The two events associated with the end of activity on the surface are nightfall and inundation. Crabs occasionally remain active on the surface 1-2 hours after dusk, but crabs remaining outside their burrows after inundation are likely to be eaten by subtidal predators (especially toadfish; see Section D, this Chapter). The importance of owning a burrow during the late period of activity is, therefore, a matter of life or death when the tide is approaching the burrow. This might explain why crabs remain closer to the burrows (the better to defend them) during the late period than during the middle period.

C. FIDELITY TO BURROWS

Methods and Materials

Fidelity of H. cordiformis to a particular burrow (i.e. duration of ownership) was assessed by two methods, both in the midmangrove zone at Woolooware Bay West. The first was used for crabs in natural, unenclosed mounds. All open burrows (of this species) in each of five mounds were assigned a number, which was written in permanent ink on a tongue-depressor inserted next to the entrance of the burrow. A map was then drawn indicating the location of burrows. There were 30-55 open burrows per mound. Crabs emerging from burrows were described with respect to sex, size (< 10 mm = small; 10-12 mm = medium; and > 12 mm= large) and other distinctive characteristics (e.g. missing or damaged chelae). Each mound was observed for 30 minutes on 10 April 1985 to establish which crab owned wnich burrow. Censuses 2 and 4 days later determined the number of burrows that unequivocally contained a different crab. 'Unequivocal' evidence was a crab of a different sex or grossly different size (small vs. large only) or a crab with both chelae when the previous burrow-owner had only one. Because chelae might change colour under certain environmental or physiological conditions (Crane 1975), colour of chelae was not used as a character of identification. Because many changes in ownership could occur between crabs of the same sex, size and physical condition, this method provided minimal estimates of the proportion of crabs changing burrows over a 48-hr period. The primary advantages of this method were that crabs were not manipulated and were free to move into or away from the mounds under observation.

The second method was used to avoid the problem of underestimation associated with the previous approach. Crabs were individually numbered and 25 individuals released into 6 mounds from which the original crabs had been removed. These mounds were enclosed by formica barriers to prevent emigration (see methods of marking and details of barriers in Chapter 2). Crabs were allowed to settle into or excavate burrows for ten days before the first census on 2 December 1985. The first census involved identification of which crabs owned which burrows. For each emerging crab, this involved inserting a tongue-depressor with the number of that crab next to its burrow. Subsequent censuses on 3 December and 5 December 1985 provided estimates of the proportion of emerging crabs that had moved to a new burrow after 24 and 48 hrs. On 6 December barriers were removed to permit assessment of fidelity of individually numbered crabs in unenclosed mounds. After 48-hrs, however, only 1-2 marked crabs emerged from three of the six sites. The majority of marked crabs were presumed to have emigrated, and an intensive search of nearby burrows produced only a few marked individuals. Several previous attempts with mark and recapture of H. cordiformis yielded similarly few recaptures. Although unmarked crabs emerged from many burrows in the previously enclosed mounds, this was not considered adequate proof of new ownership, as painted numbers were commonly lost. The few data obtained after removal of barriers, therefore, were not analysed.

Results

In unenclosed and enclosed sites, less than 70% of the burrows from which a crab emerged during the first census also had a crab emerge during the second and third censuses. For unenclosed sites, 74 crabs emerged from burrows in the five mounds on 10 April 1985. On 12 April, however, only 30

Table 7.13. Proportion of male and female *H. cordiformis* changing burrows between censuses.

A. UNENCLOSED SITES, after two 48-hr intervals. *n* = number of burrows from which a crab emerged on both days for each interval. Data are minimal estimates of the frequencies with which crabs changed burrows (see text). Each site had a total of 30-55 open burrows; data from the 5 sites have been pooled.

SEX OF INITIAL BURROW-OWNER	PROPORTION OF CRABS IN DIFFERENT BURROWS 10-12 APRIL 1985	 12-14 APRIL 1985
Male	0.43 (*n* = 7)	0.18 (*n* = 17)
Female	0.26 (*n* = 23)	0.17 (*n* = 24)

B. ENCLOSED SITES, after 24 and 48 hrs. *n* = number of crabs emerging on both days for each interval. Each site had 30-40 open burrows; data from the 6 sites have been pooled.

SEX OF INITIAL BURROW-OWNER	PROPORTION OF CRABS IN DIFFERENT BURROWS 2-3 DECEMBER 1985	 3-5 DECEMBER 1985
Male	0.82 (*n* = 22)	1.00 (*n* = 14)
Female	0.68 (*n* = 19)	0.68 (*n* = 22)

crabs emerged from these burrows, although an additional 32 crabs emerged from burrows other than the 74 used for baseline data on 10 April. On 14 April, 41 crabs emerged from the 62 burrows marked 48 hrs earlier. The numbers of crabs re-emerging after 24 and 48 hrs in enclosed sites were less than those in unenclosed sites (< 30% for 6 sites). The sizes of samples (n) that could be used to assess fidelity, therefore, were small relative to the total numbers of crabs and burrows per site (Table 7.13).

The few data that could be used suggested that the minimal proportion of crabs changing burrows during a 48-hr period was 0.17 for unenclosed crabs (Table 7.13). There was no consistent difference between sexes nor between the two 48-hr intervals sampled. These estimates were much smaller than those obtained from numbered, enclosed crabs of which 68-100% changed burrows after 24 or 48 hrs. Because unenclosed crabs were sampled in autumn and enclosed crabs were sampled during the following summer, results can not be directly compared. Analysis of variance indicated that more males than females moved to new burrows between censuses ($P < 0.025$, $F = 6.75$; 1,20 df). In fact, of the 14 males emerging on both 3 December and 5 December 1985, all had taken a new burrow during the 48-hr interval whereas only 69% of the females emerging on both days had changed burrows.

Discussion

One reason for the large differences in estimates of fidelity between crabs in unenclosed versus enclosed sites is that crabs replaced by others of the same sex and size in unenclosed sites were conservatively reported to be the same crab. The much larger apparent rate of changing burrows in enclosed sites with numbered crabs suggested that many or most crabs were replaced by crabs of the same sex and similar size. Griffin (1968) found that in 11 of 12 fights over ownership of burrows, the larger crab won. This observation suggested that new burrow-owners would be larger than the former owner. The victor in such contests, however, frequently abandoned the burrow and the former owner or another crab could then take possession. This might explain why new owners in the present study were not consistently larger than the former owners.

An alternative explanation for the greater rate of changing burrows in enclosures is that this manipulation made burrows less satisfactory for crabs, and caused them to seek new burrows more often than if they had not been enclosed (i.e. artifact of barriers). Had crabs remained in the sites subsequent to removal of the barriers, this alternative explanation could have been tested. Unfortunately, this was not the case.

In enclosures, more males changed burrows than females. Analyses of maximum distances traversed by males and females (Section B, this chapter) suggested that males might wander further from their burrows than females, and perhaps this makes their burrows more difficult to defend from intruders.

The large proportion of H. cordiformis changing burrows during a relatively short interval (24 or 48 hrs) is surprising when observations indicated that crabs remained fairly close to their burrows throughout periods of emersion (Figure 7.6) and demonstrated a variety of defensive or territorial responses triggered by the approach of a wandering crab. Nonetheless, the duration of emersion (typically at least 6 hrs) would provide ample opportunity for any crab to lose its burrow on at least one of its many excursions.

Possession of a burrow is a requirement for survival (see Section D, this Chapter). All burrows, however, probably provide similar access to the water table and refuge from predators, and crabs could survive equally well in any burrow. Given that there are usually at least a few unoccupied burrows nearby (indicated by burrows from which no crabs were seen to emerge and which were not plugged prior to submergence) and that crabs can rapidly excavate a burrow deep enough to hide in before submergence, failure to maintain a particular burrow would not, in itself, be a fatal situation.

D. ROLE OF THE BURROW AS A REFUGE FROM SUBTIDAL PREDATORS

Methods and Materials

The role of the burrow as a refuge against subtidal predators was tested in an experiment with H. cordiformis in the lower midmangrove zone at Careel Bay. The lower midmangrove zone was used to ensure that the water at high tide would be deep enough for subtidal carnivores to pass over and into bins. Examination of gut contents and the great abundance during high tide of toadfish, Tetractenos hamiltoni (Gray and Richardson), suggested that these were the most likely predators of import (Gum 1986; pers. observation). Two treatments were used, one not allowing crabs to burrow before submergence by the incoming tide and one allowing crabs to burrow. Both treatments utilised perforated plastic bins (30 cm x 45 cm x 16 cm deep). On 23 September 1985, a total of 8 bins was used. On 24 and 25 September, 12 bins were used. Half the bins were filled to a depth of 8 cm with sandy substratum from the landward zone (= Deep bins); the other half were filled to a depth of 7 cm, this layer covered with a thin sheet of plastic, and an additional 1 cm of sand added atop this plastic sheet (= Shallow bins). The latter treatment, therefore, allowed crabs to create only shallow depressions, and they could not hide beneath the substratum. The distance between the surface of the sediments in both types of bins and the top edge of the bins was adequate to prevent escape by crabs.

Sandy substratum from the landward zone was used for two reasons. In pilot experiments using the siltier sediments from the lower midmangrove zone, it was impossible to observe events inside bins after submergence by the tide because the water in them became murky with the suspension of fine-grained material. Sediments in the landward zone have less silt and more sand which does not re-suspend as easily as silts and clays. Also, the great density of peg roots and nutritive roots in the midmangrove zone made it difficult to create an even layer of sediment of the desired depth in the bins. An even layer was desired to avoid creating refuges which would have resulted from an attempt to mash root-laden sediments into the bins. Peg roots and nutritive roots are less dense in the landward zone, and peg roots could be more easily removed from these sediments. The only refuges that were possible, therefore, were ones created by the crabs themselves.

Bins were buried flush with the surface of the surrounding substratum (because toadfish are epibenthic feeders) and were arranged in two rows parallel to the shoreline. Each observer was responsible for recording events in 4 bins (2 Deep and 2 Shallow bins). Observers sat as still as possible on stools placed adjacent to bins before submergence.

One hour before submergence, 20 crabs were added to each bin. Crabs had been collected and marked in the field with a spot of white latex paint (to improve detectability in the bins) before addition to the treatments. One hour proved adequate for virtually all crabs in Deep bins to dig, enter and plug burrows before being covered by the tide. During the period of submergence, each observer recorded the numbers of crabs in each bin that were eaten and the species of predator taking each crab. At the end of the 2-hr period of observation, bins were collected, and surviving crabs were extracted from the sediments and counted. The difference between the initial numbers of crabs and the numbers that were eaten or were re-collected from bins was attributed to crabs that were missing (either because they escaped - which was unlikely - or because they were not seen being eaten).

Results and Discussion

The only subtidal predators observed during the three runs of the experiment were toadfish (10-15 cm in length). These entered the midmangrove zone close behind the tidal front within 15 minutes of submergence, although the water was only 10-15 cm deep. They entered bins and began to attack crabs almost immediately. When toadfish entered bins, crabs that were on the surface of the sediments assumed a defensive stance, with open chelae extended outwards. Because of this, fish could not immediately seize a crab but would approach from several angles until the fish could grab the crab's body while avoiding its chelae. Frequently, more than one fish would simultaneously approach a crab from different angles, and this made it easier for at least one toadfish to seize the prey. After capturing a crab, a fish would usually swim a short distance away to consume its prey, but other fish would seize legs, chelae or other parts protruding from the captor's mouth. After the crab was consumed, the fish returned to the same or another bin and attacked again. Large crabs appeared to take longer to capture than smaller crabs; however, large size did not provide a refuge for H. cordiformis.

Another frequent observation was a crab grasping the anal fin or tail of a toadfish swimming overhead, but before long other fish approached and attacked and consumed the offending crab. Toadfish entered but did not remain long in bins without crabs on the surface. Occasionally, fish stirred up the first few millimeters of sediment in such bins by blowing water or

Table 7.14. Numbers of *H. cordiformis* eaten by toadfish on 22, 23 and 24 September 1985. S = Shallow bins; D = Deep bins.

FATE OF CRABS	22 SEPT 85			23 SEPT 85			24 SEPT 85		
	S	D		S	D		S	D	
Eaten	56	15	71	104	19	123	120	16	136
Not Eaten	20	50	70	15	100	115	0	103	103
TOTALS	76	65	141	119	119	238	120	119	239
Chi-Square (1 DF)	35.89 $P < 0.001$			121.57 $P < 0.001$			182.53 $P < 0.001$		

rapidly waving the tail close to the substratum and then re-examined the surface.

In Deep bins, occasionally one or two crabs were still on the surface or re-emerged after being covered by the tide. No crabs were seen to escape.

On all three days more crabs were eaten in Shallow than in Deep bins (Table 7.14). Between 70 and 100% of the crabs in Shallow bins were consumed within two hours of submergence whereas only 13 to 19% of the crabs in Deep bins were eaten. The greatest proportion of crabs that could not be accounted for at the end of observations occurred on the first day, when 18% of the crabs in Deep bins were missing. On this day only 5% were missing from the Shallow bins, and, on the following two days, less than 1% were unaccounted for.

In conclusion, crabs remaining on the surface of the substratum (or re-emerging onto the surface) after being submerged stand a very small chance of surviving predation by toadfish. Entering and remaining in burrows during high tide, therefore, provides a refuge for H. cordiformis from toadfish and perhaps other subtidal predators.

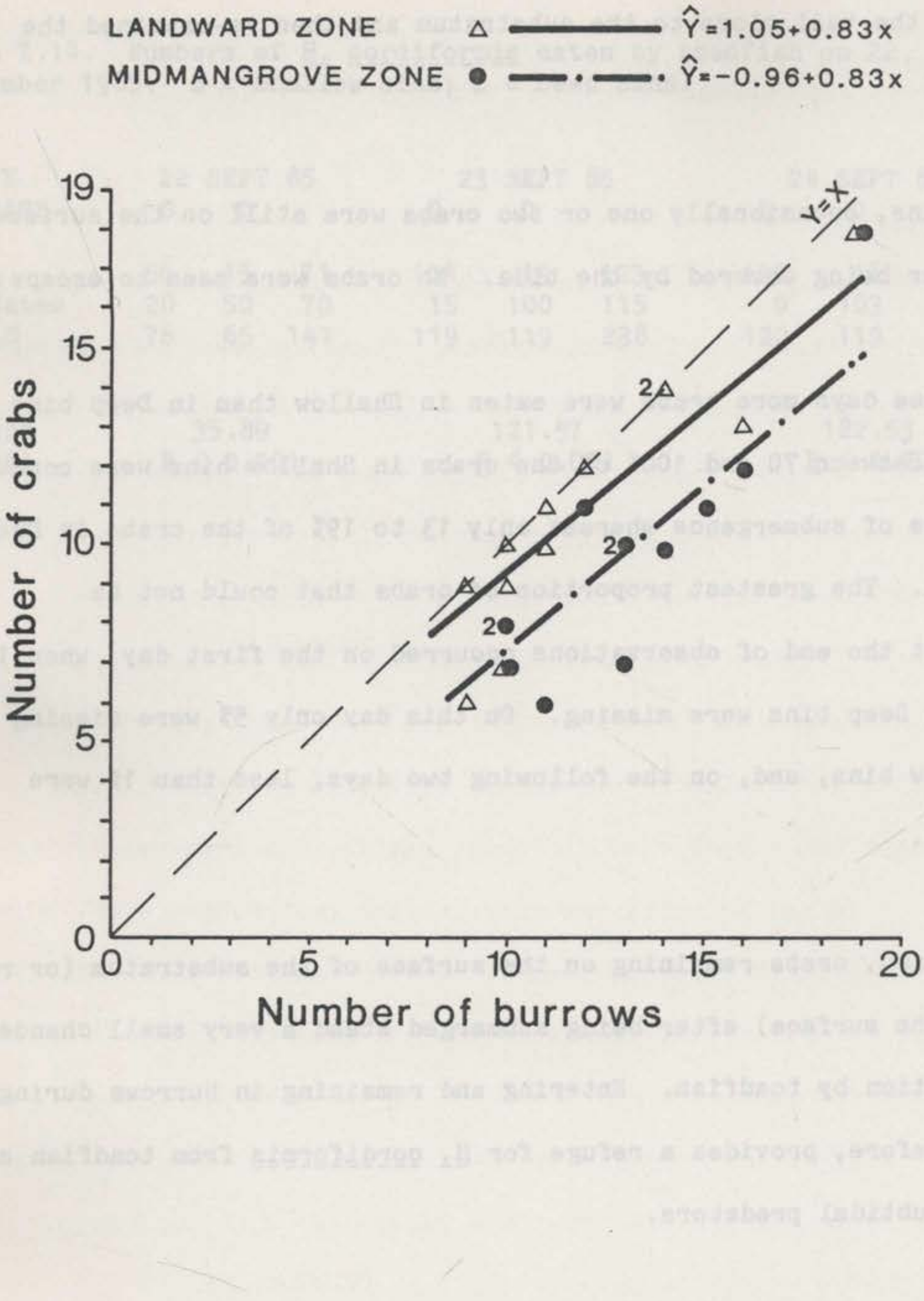

Figure 7.10. Regression of the number of crabs on the number of burrows for each zone. Periods were pooled (as this factor was not significant in the analysis of variance).

E. RELATIONSHIP BETWEEN APPARENT ABUNDANCES OF H. CORDIFORMIS AND THE NUMBER OF OPEN BURROWS

Methods and Materials

Estimates of the abundances of *H. cordiformis* and their open burrows were obtained from the 0.40 m x 0.40 m sites observed for the analysis of behaviour (Section B, this chapter). The abundances of crabs and burrows were correlated (see below), so analysis of covariance (ANCOVA) was used to detemine the effects of zone and period of activity (early vs. middle) on the relationship between the density of crabs and burrows.

Results and Discussion

Apparent abundances of crabs and numbers of open burrows were significantly correlated (combined r from ANCOVA = 0.91, $P < 0.01$, 22 df); therefore, the number of open burrows was a good predictor of the number of crabs active on the surface. The maximum number of crabs observed per burrow was 1.0, a common observation in the landward zone (Figure 7.10). The ratio of crabs to burrows was significantly greater in the landward zone than in the seaward zone, but there was no effect of period of activity (Table 7.15).

Although the numbers of *H. cordiformis* were significantly correlated with numbers of open burrows of this species, caution should be exercised in attempting to assess abundances of crabs from densities of burrows. In using direct counts of crabs to estimate abundance, visual counts of crabs assess only the numbers of crabs actively emerging from burrows. This type of measurement of abundance has, therfore, been referred to as 'apparent'

Table 7.15. Analysis of covariance of the numbers of H. cordiformis and open burrows of this species during the early and middle periods of activity in each tidal zone. Variate, y, = number of crabs; covariate, x, = number of burrows. Data were untransformed, and Cochran's test was significant ($0.01 < P < 0.05$); therefore, the criterion for significance in the analysis of covariance was set at $P = 0.01$). $n = 4$ sampling units. Slopes were not different ($F = 0.34$, $P > 0.50$, with 5,12 df).

SOURCE	DF	MS	F	P
Regression	1	173.04	78.30	< 0.001
Zones	1	27.26	12.33	< 0.005
Periods	2	1.30	0.59	> 0.50
Z x P	2	1.79	0.81	> 0.25
Residual	17	2.21		

abundance. An unknown proportion of the entire population will always be under-represented by their failure to emerge.

Crabs active on the surface will always have emerged from (and therefore opened) a burrow, but some burrows are unoccupied or contain crabs which might not emerge onto the surface. Burrows contain more than one crab only on a very short-term basis, usually when crabs are suddenly frightened and jump down the nearest burrow. Counting burrows during times of the year when *H. cordiformis* are active on the surface might, therefore, overestimate 'true' numbers of active crabs.

During winter, few open burrows of this species can be found; the crabs plug and remain in their burrows. Using counts of burrows to estimate true abundances of crabs would, therefore, be grossly inaccurate during winter and might also be somewhat inaccurate in late autumn and early spring when only a proportion of the population might be active.

CHAPTER 8. GENERAL DISCUSSION

Behaviour and spatial distributions

H. cordiformis, P. laevis and S. erythrodactyla were active on the mangrove surface only during periods of emersion. All three species occupied burrows but only H. cordiformis appeared able to excavate new burrows (it was the only species that made proper burrows in enclosures; see Chapter 5). The superior burrowing ability of ocypodids relative to grapsids has been reported in other intertidal, soft-sediment systems (Hartnoll 1965; Warner 1969; Griffin 1971; Macnae 1968). Also unlike the two grapsid species of this study, H. cordiformis remained fairly close to their burrows, and most of their activities were centred around the burrow (≤ 30 cm away). When crabs left the burrow to feed, dump excavated material or to form mud balls to take down the burrow, these activities were punctuated by returns to the burrow approximately every 10-15 minutes. Because H. cordiformis defend their burrows against wandering crabs, these frequent returns might advertise ownership and otherwise facilitate the exclusion of intruders.

Searching for and probing unattended burrows is the usual way crabs obtain new burrows (the actual act of a crab excavating a new burrow was never observed under natural conditions); therefore, wandering crabs and defensive behaviour of burrow-owners are common observations. One reason for wandering crabs settling into mounds is that burrows are most abundant in this microhabitat. The distributional pattern of H. cordiformis between mounds and flats is, therefore, largely explicable by the nature and spatial attributes of their behaviour.

Experiments confirmed that *H. cordiformis* had a strong preference for mounds and that observed natural distributions could be explained by habitat selection. When topography and the type of the sediments (material) were manipulated to examine the nature of criteria for selection, both factors were important for *H. cordiformis*.

Experiments demonstrated that *P. laevis* had a weak preference for flats but the availability of unoccupied burrows may affect habitat selection. Topography and nature of the sediments each had a significant effect on preference but not in any consistent manner.

In experiments, *S. erythrodactyla* moved into mounds and flats with similar frequency, reflecting the observed distribution of this species in mounds and flats.

Prior, subsequent or simultaneous addition of a second species to experimental enclosures did not result in distributional patterns different from those established when each species was tested alone. Interspecific interactions probably are not important in the explanation of observed distributional patterns between microhabitats.

Only a few studies have examined the effect of microtopography on small-scale spatial distributions of marine invertebrates. Core samples from crests and troughs of rippled sand flats indicated significantly greater abundances of meobenthic (infaunal) nematodes and amphipods in crests (approximately $\leq$ 10 mm in height and $\leq$ 80 mm wavelength)(Fenwick 1984; Hogue and Miller 1981). The authors suggested that nematodes are attracted to organic material and associated microbial fauna that get buried under the migrating crests instead of washed away in troughs. They did not test this model of habitat selection.

Fenwick (1984) found that one species of amphipod was more abundant in crests (approximately $\leq$ 200 mm in height and 400 mm wavelength), one species more abundant in flats and two were distributed in similar abundances between these microhabitats. In some cases, these patterns differed between sexes or between juveniles and adults. Again, mechanisms associated with these patterns were not tested but were hypothesized to be habitat selection, interspecific competition and/or differences in abiotic hydrodynamic factors between crests and troughs.

The importance of behaviour (in general) and preference (in particular) to the larger scale zonal distributions of mangrove crabs probably varies among the species of this study. Of the three species, the distributional pattern of H. cordiformis between microhabitats was the most consistent. Their preference for mounds, which are better drained and of coarser sediments than flats, would suggest a preference for the highest, most landward levels in the swamp, where the sediments are coarser and better drained than those at lower levels (Yates 1978). Five of nine censuses (3 seasons x 3 swamps), however, indicated no significant difference between abundances in the seaward and landward zone and that greatest abundances occurred in the midmangrove zone (Chapter 3). Neither their preference for mounds nor their tendency to remain close to burrows in mounds, therefore, seems very relevant to their distributions among zones.

The preference of P. laevis for moist flats might indicate a preference for the more waterlogged sediments of the lower two zones, and, in fact, this species tended to be most abundant in the seaward and midmangrove zones.

S. erythrodactyla demonstrated no significant preference for mounds or flats, and they were also distributed in similar abundances across the zones. If habitat selection is an important mechanism underlying the two scales of distribution for this species, then their lack of preference with respect to either is at least consistent.

Yates (1978) tested (in the laboratory) the importance of habitat selection to the zonal distributions he observed for H. cordiformis, P. laevis and S. erythrodactyla at one swamp near Sydney (Patonga). Results from preference experiments correlated well with the distributional patterns of H. cordiformis, but not as well for P. laevis and S. erythrodactyla. The most relevant criteria for habitat selection were degree of saturation of the substrata and to a lesser extent the particle size distribution (= texture) of the sediments.

In laboratory experiments, Griffin (1971) tested the effects of salinity, immersion, texture of the substratum and availability of cover (stones on the surface) on habitat selection of eight species of crabs from five types of shores in Tasmania. In trials testing salinity and immersion, crabs were presented with trays of freshwater and seawater but no substratum, conditions with little relevance to populations at large. Experiments with fine, medium and coarse sediments also tested preferences for submerged or emersed substrata, with and without stones. These treatments were somewhat more natural than the ones above, but each type of substratum came from a different shore; therefore, responses of crabs could be to different soil textures or to other factors intrinsic to different shores. In this latter series of experiments, several species demonstrated a tendency to occur above or below water, and most species chose to occupy substratum among stones (indicating preference for these types of microhabitats within or among shores). The ocypodids preferred sediments of medium texture (mud, as opposed to sand or 'earth'). These results did, however, suggest that behaviour might have been correlated with observed distributions.

Although several authors have suggested that habitat selection of fiddler crabs explained their zonal distributions, most of these investigations did not actually test this hypothesis experimentally (e.g. Jones and Simons 1982; Ono 1962). The few exceptions were usually done under laboratory conditions.

Teal (1958) suggested that the zonal distributions of three species of fiddler crabs reflected preferences (determined in the laboratory) for sediments of differing texture, saturation with seawater and salinity, but that interspecific interference was also important. Ringold (1979) examined the effect of the density of the root mat of Spartina alterniflora on the distribution of fiddler crabs and determined that this was probably more important than texture of sediments and other factors in explaining the zonal distributions of two species of crabs. Although Ringold (1979) attributed the results to a passive response of crabs to variation in the density of the root mat (reflecting differences in the ability of crabs to penetrate the root mat), Bertness and Miller (1984) demonstrated that preference was also important, and that the nature of the sediments and availability of artificial 'burrows' also had significant effects on habitat selection.

In summary, preference is probably the mechanism underlying distributions of crabs between microhabitats and zones in a variety of species of burrowing crabs.

Behaviour and substrata

In experiments testing preference, the relationship between crabs and the substratum was examined from the perspective of how the nature of the substratum influenced the distributions of crabs. The activities of H. cordiformis, however, could greatly affect the nature of the substratum (see Chapter 6). Deposition of excavated material onto the surface, feeding and/or forming mud balls in the fine-grained flats led to coarser-grained sediments at the surface in areas where H. cordiformis were active. By adding fiddler crabs to enclosures containing inter-bedded coloured and natural layers of sand (in the laboratory and in the field), Allen and Curran (1974) demonstrated that Uca pugilator actively mixed sediments by depositing material from the burrow onto the surface. The authors did not, however, indicate whether the texture of the sediments at the surface had been significantly affected.

The only other examination of the effect of crabs on the texture of sediments at the surface was that of Hoffman et al. (1984) on U. pugnax. They found no significant effect of the activities of this species, but their core samples may have been too deep to detect changes in the sediments within the top few millimetres - the only relevant layer with respect to feeding and forming mud balls (see Crane 1975; Fielder 1970; Miller 1961; Wada 1985).

The literature on bioturbation by intertidal, subtidal and deep-sea invertebrates is replete with examples of the effects of feeding and burrowing on the texture of sediments (see reviews by Boucout 1981; Ekdale et al. 1984; Rhoads 1974). Infaunal deposit feeders that are oriented with their mouths downward ingest only fine particles which are transported upward and deposited (as faeces) at the surface. Particles too large to be ingested remain deep in the substratum while finer sediments accumulate at the surface (e.g. Rhoads and Young 1971). Ingestion and defecation of sediments can also skew the distribution of grain-sizes toward coarser particles if mucus or other secretions compact fine material into pellets or other castings (Rhoads 1967, 1974). The texture of sediments at the surface can also be affected by selection and sorting of particles during construction of burrows (e.g. ghost shrimps and snapping shrimps; Farrow 1971; Shinn 1968).

The feeding, burrowing and other activities of H. cordiformis surprisingly had no significant effect on the concentration of organic matter in the sediments at the surface (Chapter 6). Robertson et al. (1980), however, determined that crabs are inefficient at harvesting available food and might be leaving approximately 60% of the detritus and microorganisms in substratum that has been foraged. H. cordiformis significantly reduced the percent cover of microalgae in experimental enclosures. This reduction was probably the result of ingestion but might have also reflected smothering of algae under material excavated from the burrow. Because thick algal mats were seen only occasionally under natural conditions, and these patches were usually small (approximately ≤ 1 m^2), crabs might also be limiting the abundance of microalgae throughout the swamp.

Other studies on the importance of deposit feeding crabs and grazing gastropods on microalgal abundance have reported positive, negative or no effects of these activities. Dye and Lasiak (1986) found that two species of fiddler crabs from tropical mangroves had no effect on microalgal abundance: algae were picked up and procesed with the sediments but then rejected in feeding pellets. Robertson *et al.* (1980) also found no long-term effects of *U. pugilator* on algal abundances in salt marshes. The salt marsh mud snail *Nassarius obsoleta* reduced algal biomass and productivity, probably by ingestion and not physical disturbance associated with their movements through the sediments (Pace *et al.* 1979). Darley *et al.* (in Montague 1980) suggested that mechanical disturbance to the surface of the substratum could stimulate algal growth by providing greater surface area for cells to be exposed to sunlight, by increasing availability of nutrients from increased microbial activity and providing a more favourable aerobic environment.

The most obvious effect of *H. cordiformis* on the substratum in mangrove swamps was the formation of mounds (Chapter 6). Burrowing, therefore, would increase the availability of their preferred microhabitat and this, in turn, would allow increased abundance of conspecifics. It is even possible that accretion of material into mounds might lead to a local decrease in the abundance of *P. laevis*, which preferred flats.

A few species of fiddler crabs (Uca) and ghost crabs (Ocypode) pile substratum into mounds, 'pyramids', walls, etc. near or at some distance from the burrow (Crane 1975; Lighter 1974; Zucker 1974), but these 'mounds' differ from those created by H. cordiformis in several important ways. In most cases, the material comprising the structure is collected from the surface sediments and built into some characteristic form. These structures advertise ownership of burrows or reproductive condition, reduce the size of defended territories (by obscuring neighbouring crabs from view), act as 'signposts' for orientation, and/or amplify acoustical signals (Crane 1975; Lighter 1974; Zucker 1974). These structures are small (diameter and height of a few centimetres) and probably short-lived. These topographic features are constructed by crabs and are apparently associated with a specific purpose, and do not simply represent the passive accretion of material excavated from burrows that characterises the mounds of H. cordiformis. Although fiddler crabs excavate and maintain burrows, excavated material is deposited away from the burrow (Crane 1975) and this might explain why mounds do not form around their burrows.

Mounds created by the burrowing activities of callianassids (ghost shrimps) and alpheids (snapping shrimps) are similar to those of H. cordiformis in that they form from the accumulation of excavated material from burrows (Farrow 1971; Shinn 1968). Mounds associated with alpheids are lower on the shore (seaward of mangroves and/or in seagrass beds) whereas those of callianassids have occasionally been seen as high as in the upper region of the midmangrove zone. These structures are shaped like volcanoes, represent the contribution of sediment from a single burrow, and sediments from adjacent burrows do not coalesce into larger mounds surrounding several burrows (as in H. cordiformis). Mounds from alpheid burrows are generally smaller than those of H. cordiformis and those of callianassid burrows are variable in size. The mounds of each type of burrower may be as persistent as those of H. cordiformis but probably deteriorate when the burrow is abandoned. Mounds of H. cordiformis were observed to persist throughout the year and even over winter when crabs were not active on the surface.

Infaunal, deposit-feeding polychaetes and holothurians also create mounds by the defecation of ingested sediments at the surface (see reviews by Rhoads 1974; Woodin 1983). These are usually small, volcano-shaped deposits (one per animal) and are enriched with digestive secretions, but, like the mounds of H. cordiformis, callianassids and alpheids, represent accumulations of rejected material and are not actively constructed.

Burrows and their associated structures, faecal castings and irregularities in the texture and laminations of sediment have been extensively studied from a palaeontological perspective because they provide information about ancient sedimentary conditions (see reviews by Boucot 1981; Ekdale et al. 1984; Rhoads 1974).

An equally large body of literature has examined the effects of burrowing, the biogenic formation of mounds and depressions, and other types of bioturbation on the community structure of soft-sediment environments. Studies of agents responsible for these effects span a broad range of taxa, habitats and processes, from gray whales that remove infaunal invertebrate prey from the sea floor by suction (and thus create large pits; Oliver and Slattery 1985), to rays that dig pits to expose their prey (Van Blaricom

1982), to tiny polychaetes that create faecal mounds as a by-product of deposit-feeding (e.g. Woodin 1985). These studies have demonstrated a variety of inhibitory and facilitative effects. 'Sediment destabilisers' (sensu Woodin 1983), such as mobile or sedentary deposit-feeders can adversely affect suspension-feeders because the movements or defecation of the former resuspend fine particles that clog the filtering mechanisms of the latter, or bury newly-settled larvae or interfere with settlement. These two types of functional groups, therefore, rarely occur in the same microhabitats (Aller and Dodge 1974; Brenchley 1981; Rhoads and Young 1970). Faecal mounds can also promote colonisation. The mounds produced by the holothurian Molpadia oolitica promoted the settlement and growth of three suspension feeders (amphipods, polychaetes, and bivalves). Uncompacted faeces collected in the flat areas between mounds and formed an unstable surface, easily resuspended. The faecal mounds, themselves, however, provided a relatively stable surface (Rhoads and Young 1970). In actively-accruing faecal mounds of enteropneusts, harpacticoid copepods were significantly less abundant than in sediments away from mounds (Thistle 1980). Recolonisation of inactive mounds was rapid and background densities of 14 species were reached within 24 hours. Two species, however, became disproportionately abundant, and this was attributed to exploitation of unoccupied habitat.

The stabilisation of sediments by dense assemblages of tube-building worms can also increase abundance and diversity of other benthic organisms (Aller and Aller 1986; Bailey-Brock 1979; Macnae and Kalk 1962; Wilson 1979). Burrows and tubes constructed by one organism are frequently shared with or taken over by other organisms (e.g. scale worms in burrows of lugworms, Reise 1985). The flushing of sediments (for example by the feeding currents of infaunal bivalves) and nutrient-enrichment of sediments can also promote the settlement and growth of other organisms (Gallagher et al. 1983). If these effects result in an increase in microbial production ('gardening', sensu Hylleberg 1975), then benthic grazers, deposit-feeders and other organisms that do not cause excessive bioturbation can instead promote the abundance of food in their microhabitat (e.g. Connor et al. 1982).

Although the present study did not examine the influence of burrowing, feeding and other activities of H. cordiformis on meiofauna, field experiments with fiddler crabs have indicated significant inhibitory or promotive effects. Nematodes were more abundant near the burrows of U. pugnax than away from these structures, but the opposite pattern was seen for copepods (Bell et al. 1978). The authors suggested (but did not test) that the increase in nematodes might have resulted from nutrient enrichment and subsequent microbial growth ('gardening') around the burrow. The cause of the decrease in copepods was not explained.

The removal of U. pugnax from experimental enclosures and/or reduction of their abundance from large pens resulted in significant increases in nematodes, meiofaunal crustaceans (primarily copepods but also larvae) and annelids relative to enclosures with crabs (Hoffman et al. 1984). These results might have been in response to the greater oxygenation of sediments measured in enclosures with crabs and were probably not related to increased nutrients. The authors attributed these effects to deposit-feeding (and direct removal of meiofauna by ingestion) rather than bioturbation associated with burrowing. Their explanation, was, however, discounted by Dye and

Lasiak (1986) who examined gut contents of U. vocans and U. polita and found no evidence that meiofauna were ingested although they, too, observed significant increases in meiofaunal abundances when crabs were excluded from areas of substratum. Because meiofaunal concentrations in feeding pellets were small relative to those in the surrounding sediments, meiofauna (primarily nematodes) were not being collected in the sediments and subsequently rejected, but were not picked up at all during foraging. Dye and Lasiak suggested that because vertical migration of meiofauna is a well-documented phenomenon (Dye 1978; McLachlan et al. 1977), bioturbation of the sediments by crabs feeding or foraging might stimulate downward migration of meiofauna where they might also encounter a refuge from ingestion by crabs. Vertical migrations within sediments might alternatively be the result of endogenous activity rhythms (e.g. Eaton and Simpson 1979; Gamble and Keeble 1903; Palmer and Round 1967).

From the above discussion on the relationship between behaviour, distributions and the nature of the mangrove substratum, it is evident that crabs both affect and are affected by their environment. H. cordiformis chose to occupy extant mounds but created and increased the availability of their preferred microhabitat by excavating burrows and depositing material from this activity on the surface. The bioturbation caused by burrowing and feeding was shown to reduce algal abundances. These activities might reduce or increase microbial and meiofaunal production which, in turn, might affect the availability of these sources of food. The enhancement by fiddler crabs of standing stocks of Spartina spp. has been demonstrated by Bertness (1985) and Montague (1982), but analogous positive effects of mangrove-dwelling ocypodids on mangrove vegetation have not been investigated. In fact, although the investigation of energy flow and trophic structure of Australian mangrove ecosystems has received increasingly more attention during the past decade, the nature of trophic structure and energy flow is still largely unknown (Redfield 1982). Quantitative information on the trophic relationships of local mangrove crabs was obtained for only one species (*H. cordiformis*) and for two potential effects, algal abundance and concentration of organic matter in surface sediments.

Behaviour and the functions of the burrow

The importance of burrows to crabs in intertidal and supratidal environments is suggested by the prevalence of this association in a wide range of habitats: mudflats, seagrass beds, saltmarshes, mangrove swamps, coastal dunes and even grasslands up to 5 km from the shore (Warner 1977). Experimentally tested or inferred functions of the burrow include refuges from subtidal, terrestrial or avian predators, refuges from environmental stresses (primarily desiccation in intertidal and supratidal species), centres for courtship, defence of territories and other behaviours, and sites for incubation and extrusion of eggs (see review by Montague 1980). Although many crabs do not, or cannot, construct their own burrows, most crabs are associated with these structures.

The role of the burrow as a refuge against subtidal predators was convincingly demonstrated for *H. cordiformis* (Chapter 7). Burrows probably function in the same way for *P. laevis* and *S. erythrodactyla*. The use of direct observation of predation in this experiment (and supportive evidence from gut contents of toadfish) allowed identification of the most important predator.

During emersion, burrows may provide a refuge against terrestrial and avian predators. No mammalian predators of crabs are known for swamps in New South Wales, although the rat *Xeromys myoides* is believed to be a predator of crabs in mangrove swamps in northern Australia (Magnusson *et al.* 1976).

Like the mammals, reptiles tend to be more common in tropical mangroves than in swamps of New South Wales. Snakes and lizards can also occur in mangroves as their primary or secondary habitat, and various species feed on crabs (e.g. the snake *Acrochordus granulatus*, Cogger 1979).

In local swamps, the most likely predators of import during periods of emersion are the wetland avifauna, including herons, ibises, whimbrells, plovers, curlews and terns (Hutchings and Recher 1974). Several species are documented predators of fiddler crabs (Boshe 1982; Colby and Fonseca 1979; Zwarts 1985; and many others). Local species tend to forage primarily in the seagrass beds and mudflats seaward of the mangrove proper, but have also been observed (especially ibises) probing the substratum in the midmangrove and landward zones. Shore birds might selectively feed on crabs of a certain size class or in areas where crabs of a particular range of sizes are most abundant or most accessible (by virtue of the zone-specific depths to which they burrow; Boshe 1982; Zwarts 1985). This, in turn, could influence the distribution of size classes.

When emersed, crabs respond to movements (e.g. an approaching bird or observer) by rapidly jumping into an open burrow. The entry of crabs into their burrows before submergence is, however, not a direct response to the arrival of any immediate threat, but to a particular phase of the tidal cycle. The latter type of behaviour allows crabs to obtain a refuge before the arrival of their subtidal predators, and can therefore be considered 'avoidance' rather than escape (see other examples for gastropods in Garrity and Levings 1983; Hamilton 1976; Levings and Garrity 1983,1984; Warren 1985; Wells 1980).

Refuge against stressful environmental conditions is another major function of burrows. Although not examined in the present study, this has been demonstrated for fiddler crabs. Burrows protect crabs against adversely high or low ambient temperatures (Powers and Cole 1976; Smith and Miller 1973; Whiting and Moshiri 1974; Wilkens and Fingerman 1965) and provide a source of water (or at least moisture) during periods of emersion (Aspey 1978; Crane 1975). While active on the surface, all crabs experience loss of water via evapotranspirative cooling, but deposit-feeding crabs that rely on branchial water for sorting food from sediment also lose water in rejected feeding pellets (Miller 1961). Burrows need not descend below the water table to allow crabs to replenish branchial water, because many crabs have tufts of hydrophilic setae that are capable of extracting water from damp substrata (Hartnoll 1973; Powers 1975; Wolcott 1984).

For crabs that excavate, maintain and defend burrows (mostly ocypodids, but also some grapsids and gecarcinids), the burrow is the centre of the defended territory, and the site where courtship and copulation occur for many species (Crane 1975; Griffin 1971; Warner 1977). In H. cordiformis, courtship occurs at a female's burrow and is frequently initiated by a male owning a burrow nearby (Chapter 7). Copulation might take place outside or inside the burrow. In a large number of fiddler crabs, reproductive males hold burrows in a particular area of the swamp (usually high on the shore) and wave to attract females into their burrows (Christy 1982b; Christy and Salmon 1984; Crane 1975; Hyatt 1977; Salmon 1983). Reproductive male H. cordiformis may also engage in waving outside the burrow, but observed copulations were all outside the female's burrow (Griffin 1968; Chapter 7, this study). Extrusion and incubation of eggs also occur in the burrow. Male grapsids may also wave or use other displays to attract females to their burrows (Hartnoll 1969; Seiple and Salmon 1982).

Various functions of the burrow have been tested or inferred from observations of ocypodids (see reviews by Crane 1975; Montague 1980; Warner 1977). Similar studies (and even general behavioural descriptions) of grapsids are few but most authors indicate that excavation, maintenance and defense of burrows are not widely observed in this family (Hartnoll 1965; Macnae 1968; Warner 1969, 1977). For the few species known to make and defend burrows, behaviours and functions associated with the burrow are similar to the patterns discussed above for H. cordiformis, fiddler crabs and other ocypodids (Crichton 1960; Seiple and Salmon 1982).

Behaviour and cyclical changes in the environment

There have been many studies of behavioural rhythmicity of intertidal invertebrates with respect to night and day, periods of emersion and submergence or longer cycles (e.g. lunar, seasonal cycles). Descriptions of these patterns have been, for the most part, qualitative. Most of the quantitative studies of rhythmic behaviour have been examinations in the laboratory of exogenous and endogenous mechanisms responsible for expression of behaviour (see reviews by DeCoursey 1976, 1983; Naylor and Hartnoll 1979;

Palmer 1974). The emphasis of the present study was to provide a quantitative description of the effects of daily and tidal cycles on the apparent abundances of H. cordiformis, P. laevis and S. erythrodactyla and also on the activities of H. cordiformis (the most easily-observed species).

Activity on the surface only during periods of emersion has been demonstrated for all ocypodids and some grapsids (Warner 1977). Carcinus maenas, one of the most extensively studied species of intertidal crabs (see review by Naylor and Hartnoll 1979), are active when submerged, possibly reflecting their phylogenetic affinity with the Portunidae - the swimming crabs. The grapsids S. reticulatum and Helice crassa and the ocypodid Macrophthalmus hirtipes are also active when submerged or emersed (Seiple and Salmon 1982; Williams et al. 1985).

Activity during emersion provides a temporal refuge from subtidal predators. Toadfish were the most likely predator of import in the present study (Chapter 7). In salt marshes along the Gulf of Mexico and the eastern coast of the United States, blue crabs (Callinectes sapidus) are probably the most important subtidal predators of fiddler crabs and have been seen to dash up to 1 m onshore to capture these ocypodids (Herrnkind 1968). Limiting their period of activity on the surface to times of emersion, however, protects the large majority of fiddler crabs from this predator.

H. cordiformis and most fiddler crabs are primarily diurnal (Crane 1975; Griffin 1968; Warner 1977; Chapter 7, this study). Densities of P. laevis and S. erythrodactyla on the surface during diurnal and nocturnal periods of emersion were not significantly different. These results are contrary to the generalisation of Hutchings and Recher (1981) that during diurnal low tides crabs tend to remain in their burrows.

The emphasis on diurnal activity in the ocypodids is probably related to their social behaviour which depends, to a large extent, on visual signals such as waving and standing guard at burrows (Crane 1975). Diurnal activity, however, might expose crabs to a greater risk of predation by their visually-hunting avian predators (Boshe 1982; Zwarts 1985). Another easily-tested advantage of diurnal activity might be a greater facility in navigating back to the burrow during the day relative to the night.

Of the two types of cycles, tidal and day/night, the former is more important to survival than the latter. This is suggested from the observations that P. laevis and S. erythrodactyla and even some H. cordiformis are active at night whereas no crabs were ever seen on the surface during submergence and few crabs can survive predation from toadfish (Chapter 7).

Within a given period of emersion, neither the number of crabs on the surface nor the nature of the activities of H. cordiformis differed significantly among the early, middle and late periods of activity (Chapter 7). A similar pattern was observed in the nature of the behaviour of Macrophthalmus hirtipes: there were only minor and inconsistent fluctuations in the proportions of time spent in various behaviours among three periods of activity during emersion (Henmi 1984). The apparent abundances of crabs from the early to middle and late periods of activity did, however, vary seasonally with a more gradual increase to maximal densities or decrease to zero during the cooler months (see discussion below).

H. cordiformis in Tasmania showed a similar pattern of emergence to local populations in that maximal densities were observed shortly after emergence of the first few crabs. Griffin (1968) indicated, however, that their behaviour progressed through a more or less consistent sequence of activities: feeding for the first hour, then displaying or wandering, with forming mud balls only toward the end of the period of emersion.

Maximal densities of another estuarine ocypodid, *Dotilla fenestrata*, were reached after a slightly longer interval (after emergence of the first few crabs) than that of *H. cordiformis*: $\geq$ 1 hr for *D. fenestrata* and $\leq$ 0.5 hr for *H. cordiformis* (Hartnoll 1973; the present study). For both species, termination of activity on the surface before a rising tide was well synchronised, with most crabs entering and plugging burrows within 0.5 hr of submergence. Hartnoll (1973) suggested that for females and small males, the sequence of activities followed a regular progression, although the order of activities differed somewhat: maintenance of the burrow, then feeding, then a combination of the two. Larger males did not follow such a rigid sequence and wandered from the burrow to engage in social activity (e.g. courtship).

Other workers have suggested that activities occur in a regular sequence, but their observations have not often been quantified. (Crane 1975; Fielder and Jones 1978; Warner 1977). Apparent differences between *H. cordiformis* in the present study and in that of Griffin (1968) and other authors might, therefore, reflect differences associated with different swamps, different species or merely different methods of assessing the prevalence of behaviour throughout the period of activity.

Although crabs engage in a number of different activities each day, Crane (1958) suggested that for the fiddler crab Uca maracoani one activity might dominate on a given day or over several days. She referred to these dominant behaviours as 'phases'. Feeding and maintenance of burrows were the commonest dominant phases of the fiddler crabs she studied, but sometimes social phases were dominant (e.g. maximal waving activity around the time of new and full moons). Frequently in the present study, the proportions of time H. cordiformis spent in various activities differed significantly among days of sampling (Chapter 7). This result might have reflected differing phases of dominant activity among days of censusing, or, simply, lack of temporal consistency.

Semilunar patterns in reproductive activity (especially hatching of eggs and release of larvae) have been described for many crabs (e.g. Christy 1978; Crane 1958; DeCoursey 1976; Naylor and Hartnoll 1979; Zucker 1976). Non-reproductive activities might also be characterised by this type of rhythmicity (Henmi 1984; Naylor 1958; Palmer 1967; Salmon 1984; Zucker 1974). There was no direct evidence for any regular semi-lunar patterns in H. cordiformis, but the 6-week behavioural study did not allow replication of observations among the lunar phases. The presence of such a behavioural cycle, therefore, could not be properly tested.

The importance of annual environmental changes (e.g. seasons) to patterns of behaviour of H. cordiformis is demonstrated most strikingly by the absence of crabs from the surface throughout winter (Griffin 1968; Yates 1978; Chapter 7). Some species of fiddler crabs (e.g. U. arcuata) also hibernate (Crane 1975). Another indication of seasonality in H. cordiformis was the longer interval between the onset of emersion (or dawn) and the initial emergence of crabs onto the surface in late autumn relative to spring. Other ocypodids, such as U. vocans and Macrophthalmus hirtipes demonstrated a similar pattern of immediate emergence after emersion in summer and delayed emergence in cooler seasons (Henmi 1984; Nakasone 1982).

Reproductive behaviour varies seasonally in most temperate species of crabs, with maximal prevalence and intensity usually in the warmer months (Warner 1977). Although temperate species of fiddler crabs wave and attempt copulation from spring through autumn, successful mating is limited to one or two months (Crane 1975). Courtship in H. cordiformis in Tasmania was observed only in summer and coincided with a maximum in the prevalence and intensity of combat (Griffin 1968). Wandering en masse (also called 'droving' or 'herding' behaviour), by which large aggregations move down from the upper shore to feed near the seaward edge, has been observed only from spring through autumn in the ocypodids Macrophthalmus hirtipes and Uca vocans (Henmi 1984; Nakasone 1982). Fidelity of emerging U. vocans to a particular burrow was suggested to last longer during winter, and storage of mud balls was seen only during this season (Nakasone 1982). Carcinus maenas, one of the few intertidal portunids, migrated offshore during winter and lost much of the circadian and circatidal behavioural patterns they demonstrated at other times of the year (Naylor et al. 1971). A similar loss of tidal rhythmicity in locomotor activity was noted for Hemigrapsus edwardsi in winter (Williams 1969). Enright (1974) suggested that seasonal changes in behaviour are probably environmentally induced and not the result of endogenous, circannual clocks.

Tidal, daily, semilunar and longer behavioural periodicities have been extensively examined for a variety of other intertidal and subtidal invertebrates (see reviews by DeCoursey 1976, 1983; Naylor and Hartnoll 1979; Palmer 1974; Saunders 1977). Most of these studies, involving observations of animals under natural conditions in the field or manipulated conditions in the laboratory, focused on isopods and amphipods on high-energy beaches or on gastropods on exposed rocky shores.

Fewer studies of behavioural rhythmicity have been done on rocky intertidal species. The major advantages of tidal and daily patterns of activity in gastropods have been correlated with the avoidance of subtidal predators during high tide (primarily fish) and/or avoidance of desiccation and high temperatures during periods of diurnal emersion (neritids, Levings and Garrity 1983; pulmonate limpets, Garrity and Levings 1983 and Levings and Garrity 1984; and coiled, predatory gastropods, Garrity 1984). Moran (1985) and Zann (1973) reported tidal rhythmicity in the foraging and sheltering behaviour of a variety of gastropods.

Several of the functions associated with tidal, daily or other patterns of activity in amphipods, isopods and gastropods are clearly irrelevant to the patterns of activity demonstrated by brachyuran crabs. Rocky intertidal gastropods on smooth surfaces, for example, must avoid desiccation by limiting foraging to periods when the substratum is damp or submerged. Although moist or submerged crevices may be present, frequent returns to replace water loss might not be feasible given their relatively slow rates of foraging and locomotion. Crabs that inhabit burrows in soft-sediments, however, have a readily available source of moisture during periods of emersion and can frequently return to burrows to replenish reserves of branchial water. Crabs, then, need not restrict their activity on the surface to periods around or during submergence, a time when the risk of predation from subtidal carnivores might be very great.

Most semilunar behavioural cycles in crabs are associated with courtship and hatching of eggs, probably to take advantage of tidal conditions for larval dispersal from or retention in the estuary (Christy 1978; Christy and Salmon 1984; DeCoursey 1979; Zucker 1976). They are not active during submersion and have greater control over their distributions than isopods and amphipods; therefore, their distributions among zones or between microhabitats are not dependent on time of locomotory behaviour relative to semilunar tidal cycles.

A unifying feature of the rhythmic behaviours exhibited by crabs, isopods, amphipods, gastropods and other intertidal and subtidal invertebrates is that most of them are controlled by endogenous 'biological clocks' (see reviews by DeCoursey 1976, 1983; Naylor and Hartnoll 1979). Because of the great diversity in the habits and habitats of these organisms, however, the functions or advantages associated with the various behavioural periodicities would be expected to differ, and, in fact, this has been demonstrated for many behavioural patterns.

Comparison of the behaviour of *H. cordiformis* and fiddler crabs

The genus *Uca* is a speciose and ubiquitous group whose members display considerable behavioural variability. On the basis of her extensive work with species worldwide, Crane (1957) characterised the genus as a spectrum ranging between two general categories of morphology, physiology and behavioural patterns: the 'narrow-fronted' species living in lower, muddier zones and demonstrating simpler social and non-social behaviours and the 'broad-fronted' species living in higher, sandier zones and demonstrating more complex behaviours. On the basis of his analyses of reproductive and other behaviours of *H. cordiformis* in eastern Tasmania, Griffin (1968) suggested that this species behaved like a narrow-fronted species of *Uca* (especially with respect to reproductive behaviour). Observations of *H. cordiformis* in mangrove swamps in the Sydney region of New South Wales also suggest a greater affinity with the narrow-fronted species (although the detailed behavioural observations of the present study were made after the season of maximal mating activity). Unlike many of the broad-fronted species, *H. cordiformis* did not follow the receding tide to feed in the lower zones and instead fed close to the burrow. Herrnkind (1968) and Crane (1975) suggested that the paucity of microorganisms and other food in the upper sandy zones dominated by the broad-fronted species might underlie their seaward feeding migrations to lower zones where food is more abundant. Because *H. cordiformis* did not wander far from their burrows and, in general, were not restricted to a particular zone on the shore, the ability to navigate back to a particular area of the swamp via 'sun compass' orientation (demonstrated for two species of broad-fronted fiddler crabs, Altevogt 1963 (in Crane 1975) and Herrnkind 1968) is probably irrelevant to *H. cordiformis*. The typically muddier substrata in mangrove swamps probably support a greater abundance of food than the shores dominated by broad-fronted species.

Similar to most narrow-fronted fiddler crabs, H. cordiformis mated on the surface, with males initiating copulation at a female's burrow (Griffin 1968; Chapter 7, this study). This is in contrast to broad-fronted species in which males occupy burrows toward the landward edge of the population, wave continuously to attract wandering females into their burrows and copulate within the burrow (Crane 1975). This behaviour results in polygynous mating by males whereas females mate only once for each clutch of eggs. The mating system of narrow-fronted fiddler crabs and H. cordiformis is 'promiscuous', with each sex mating with many individuals and the production of multiple clutches of eggs between matings (Salmon 1984).

The vertical wave of H. cordiformis is more characteristic of the narrow-fronted fiddler crabs than the typical lateral wave of the broad-fronted species (Griffin 1968). In addition, acoustical signalling to attract females has been reported only for broad-fronted species (Crane 1975).

The breeding burrows of broad-fronted fiddler crabs may have multiple terminal chambers for mated females incubating their eggs (Christy 1982). The burrows of H. cordiformis usually have only one enlarged terminal chamber (Griffin 1968).

With respect to most other activities and from a general behavioural perspective, fiddler crabs and H. cordiformis are more or less alike relative to other ocypodids (and, indeed, other families of crabs). *H. cordiformis* and fiddler crabs use a similar method to excavate and maintain burrows, and the mechanics associated with feeding are similar. All are active during periods of diurnal emersion, although some species of fiddler crabs are also active at night, and behaviour might also be mediated by longer environmental periodicities. All of these species consume algae, bacteria, meiofauna and detritus from the sediments and are themselves consumed by subtidal, terrestrial and avian predators. Because they are typically one of the most abundant groups of macrofauna (with molluscs) on estuarine shores, they probably comprise an important component of the trophic structure of these ecosystems.

The distributional patterns of *H. cordiformis*, *P. laevis* and *S. erythrodactyla* between microhabitats are largely the result of habitat selection for various characteristics of the substratum. The zonal distributions of fiddler crabs are probably explicable by the same mechanism. In addition to these effects of the substratum on distributions and abundances, fiddler crabs and *H. cordiformis* also affect the characteristics of the substratum in their habitats. The relationship between these organisms and their habitats, therefore, is characterised by significant and dynamic interactions, and largely the result of the behavioural patterns of these species.

Appendix 3

APPENDICES TO CHAPTER 3: IDENTIFICATION OF DISTRIBUTIONAL PATTERNS

Appendix 3

Appendix 3.1. Analyses of variance of distributional data from zonal censuses. SU = Sampling Unit (see text for definition). Factors were re-tested against the residual in all analyses indicating that this was justified (i.e. when full-model denominators, SU and/or SPxSU, were not significant, $P > 0.25$); the P' values correspond to tests against the residual.

A. DECEMBER 1982 - TRAPS. Data were transformed to ln (x+1); Cochran's test was not significant, $P > 0.05$. $n = 3$ traps.

SOURCE	DF	MS	F	P
Mangrove	2	0.02	0.06	> 0.50
Species	1	0	0	> 0.50
Zone	2	0.42	1.35	> 0.25
MAxSP	2	0.16	0.52	> 0.50
MAxZ	4	0.10	0.32	> 0.50
SPxZ	2	0.74	2.39	> 0.10
MAxSPxZ	4	0.14	0.45	> 0.50
Residual	36	0.31		

B. MAY 1983 - TRAPS. Data were transformed to ln (x+1); Cochran's test was not significant, $P > 0.05$. $n = 4$ traps.

SOURCE	DF	MS	F	P	P'
Mangrove	2	1.48	4.35	< 0.05	
Species	1	5.06	23.00	< 0.001	< 0.001
Zone	2	2.59	7.62	< 0.025	
MAxSP	2	2.16	9.82	< 0.01	< 0.001
MAxZ	4	0.89	2.62	> 0.10	
SPxZ	2	2.27	10.32	< 0.005	< 0.001
MAxSPxZ	4	0.75	3.41	> 0.05	< 0.025
SU(MAxZ)	9	0.34	1.55	> 0.10	
SPxSU(MAxZ)	9	0.22	1.00	> 0.25	
Residual	108	0.22			

C. MAY 1983 - QUADRATS. Data were transformed to $x^{0.25}$; Cochran's test was not significant, $P > 0.05$. $n = 4$ quadrats.

SOURCE	DF	MS	F	P
Mangrove	2	1.57	1.64	> 0.10
Species	1	79.71	113.87	< 0.001
Zone	2	6.47	6.73	< 0.025
MAxSP	2	1.35	1.93	> 0.10
MAxZ	4	6.79	7.07	< 0.01
SPxZ	2	3.61	5.16	< 0.05
MAxSPxZ	4	4.79	6.84	< 0.01
SU(MAxZ)	9	0.96	2.59	< 0.01
SPxSU(MAxZ)	9	0.70	1.89	> 0.05
Residual	108	0.37		

Appendix 3

Appendix 3.1. (Cont'd.)

D. JULY 1983 - TRAPS. Data were transformed to ln (x+1); Cochran's test was not significant, P > 0.05. n = 3 traps.

SOURCE	DF	MS	F	P
Mangrove	2	6.98	12.46	< 0.001
Species	1	72.29	124.64	< 0.001
Zone	2	14.63	26.13	< 0.001
MAxSP	2	9.03	15.57	< 0.001
MAxZ	4	0.31	0.56	> 0.50
SPxZ	2	12.40	21.38	< 0.001
MAxSPxZ	4	0.40	0.69	> 0.50
SU(MAxZ)	27	0.56	4.31	< 0.001
SPxSU(MAxZ)	27	0.58	4.46	< 0.001
Residual	144	0.13		

***JULY 1983 - QUADRATS. Only 4 crabs were seen on the surface during sampling in this month; therefore, no analyses were done.

E. OCTOBER 1983 - TRAPS. Data were transformed to ln (x+1); Cochran's test was not significant, P > 0.05. n = 3 traps.

SOURCE	DF	MS	F	P
Mangrove	2	2.70	4.43	< 0.025
Species	1	25.39	44.54	< 0.001
Zone	2	4.50	7.38	< 0.005
MAxSP	2	14.54	25.51	< 0.001
MAxZ	4	0.29	0.48	> 0.50
SPxZ	2	0.80	1.40	> 0.25
MAxSPxZ	4	1.95	3.42	< 0.025
SU(MAxZ)	27	0.61	2.26	< 0.005
SPxSU(MAxZ)	27	0.57	2.11	< 0.005
Residual	144	0.27		

F. OCTOBER 1983 - QUADRATS. Data were transformed to ln (x+1); Cochran's test was not significant, P > 0.05. n = 3 quadrats.

SOURCE	DF	MS	F	P
Mangrove	2	1.53	2.43	> 0.05
Species	1	51.43	120.43	< 0.001
Zone	2	12.35	19.66	< 0.001
MAxSP	2	1.11	1.59	> 0.05
MAxZ	4	0.90	1.43	> 0.05
SPxZ	2	8.04	18.84	< 0.001
MAxSPxZ	4	0.58	1.35	> 0.05
SU(MAxZ)	27	0.63	2.17	< 0.01
SPxSU(MAxZ)	27	0.43	1.48	> 0.05
Residual	144	0.29		

Appendix 3.1. (Cont'd.)

G. JANUARY 1984 - TRAPS. Data were transformed to ln (x+1); Cochran's test was not significant, *P* > 0.05. *n* = 3 traps.

SOURCE	DF	MS	F	*P*
Mangrove	2	1.75	3.13	> 0.05
Species	1	0.05	0.08	> 0.50
Zone	2	9.65	17.23	< 0.001
MAxSP	2	0.56	0.95	> 0.25
MAxZ	4	1.26	2.25	> 0.05
SPxZ	2	3.79	6.43	< 0.01
MAxSPxZ	4	2.97	5.03	< 0.005
SU(MAxZ)	27	0.56	1.81	< 0.01
SPxSU(MAxZ)	27	0.59	1.90	< 0.005
Residual	144	0.31		

H. JANUARY 1984 - QUADRATS. Data were transformed to ln (x+1); Cochran's test was not significant, *P* > 0.05. *n* = 3 quadrats.

SOURCE	DF	MS	F	*P*
Mangrove	2	1.43	3.58	< 0.05
Species	1	67.88	165.56	< 0.001
Zone	2	12.12	30.30	< 0.001
MAxSP	2	2.99	7.29	< 0.005
MAxZ	4	1.40	3.50	< 0.025
SPxZ	2	4.28	10.44	< 0.001
MAxSPxZ	4	0.75	1.83	> 0.10
SU(MAxZ)	27	0.40	1.48	> 0.05
SPxSU(MAxZ)	27	0.41	1.52	> 0.05
Residual	144	0.27		

Appendix 3

Appendix 3.2. Analyses of variance of distributional data from censuses of microhabitats (mounds and flats) at Careel Bay. SU = Sampling Unit (see text for definition). Factors were re-tested against the residual in all analyses indicating that this was justified (i.e. when full-model denominators, SU and/or SPxSU, were not significant, $P > 0.25$); the *P'*-values correspond to tests against the residual.

A. MAY 1983 - TRAPS. Data were transformed to ln (x+1), and Cochran's test was not significant, $P > 0.05$. $n = 4$ traps.

SOURCE	DF	MS	F	*P*	*P'*
Species	1	0.59	4.54	= 0.10	> 0.05
Zone	1	1.37	19.57	< 0.025	< 0.025
Microhabitat	1	0.91	13.00	< 0.025	< 0.05
SPxZ	1	0.86	6.62	> 0.05	< 0.05
SPxMH	1	5.09	39.15	< 0.001	< 0.001
ZxMH	1	0.38	5.43	> 0.05	> 0.10
SPxZxMH	1	3.21	24.69	< 0.01	< 0.001
SU(MHxZ)	4	0.07	0.33	> 0.50	
SPxSU(MHxZ)	4	0.13	0.62	> 0.50	
Residual	64	0.21			

B. MAY 1983 - QUADRATS. Data were transformed to $x^{0.25}$, and Cochran's test was not significant, $P > 0.05$. $n = 4$ quadrats.

SOURCE	DF	MS	F	*P*	*P'*
Species	1	5.11	39.31	< 0.005	< 0.001
Zone	1	3.27	14.86	< 0.025	< 0.001
Microhabitat	1	15.49	70.41	< 0.005	< 0.001
SPxZ	1	0.13	1.00	> 0.25	> 0.25
SPxMH	1	11.72	90.15	< 0.001	< 0.001
ZxMH	1	0.18	0.82	> 0.25	> 0.25
SPxZxMH	1	0.29	2.23	> 0.10	> 0.10
SU(MHxZ)	4	0.22	1.22	> 0.25	
SPxSU(MHxZ)	4	0.13	0.72	> 0.50	
Residual	64	0.18			

C. JULY 1983 - TRAPS. Data were untransformed, and Cochran's test was not significant, $P > 0.05$. $n = 3$ traps.

SOURCE	DF	MS	F	*P*	*P'*
Species	1	0.33	1.27	> 0.25	> 0.25
Microhabitat	1	1.33	2.05	> 0.10	> 0.10
SPxMH	1	4.08	15.69	< 0.01	< 0.025
SU(MH)	6	0.65	1.00	> 0.25	
SPxSU(MH)	6	0.26	0.40	> 0.50	
Residual	32	0.65			

Appendix 3.2. (Cont'd.)

**JULY 1983 - QUADRATS. Only 4 crabs were seen on the surface of the substratum during sampling in this month; therefore, no analysis was done).

D. OCTOBER 1983 - TRAPS. Data were transformed to $x^{0.25}$, and Cochran's test was not significant, $P > 0.05$. $n = 3$ traps.

SOURCE	DF	MS	F	P
Species	1	0.15	0.26	> 0.50
Microhabitat	1	0.59	4.21	> 0.05
SPxMH	1	0.46	0.79	> 0.25
SU(MH)	6	0.14	1.27	> 0.10
SPxSU(MH)	6	0.58	5.27	< 0.001
Residual	32	0.11		

E. OCTOBER 1983 - QUADRATS. Data were transformed to ln (x+1), and Cochran's test was not significant, $P > 0.05$. $n = 3$ quadrats.

SOURCE	DF	MS	F	P
Species	1	8.75	16.53	< 0.01
Microhabitat	1	1.89	4.60	> 0.05
SPxMH	1	12.54	23.71	< 0.01
SU(MH)	6	0.41	2.53	< 0.05
SPxSU	6	0.53	3.26	< 0.025
Residual	32	0.16		

F. JANUARY 1984 - TRAPS. Data were untransformed, and Cochran's test was was not significant, $P > 0.05$. $n = 3$ traps.

SOURCE	DF	MS	F	P	P'
Species	1	0.19	0.05	> 0.50	
Microhabitat	1	9.19	4.38	> 0.05	< 0.05
SPxMH	1	58.52	13.97	< 0.01	
SU(MH)	6	2.10	1.11	> 0.25	
SPxSU(MH)	6	4.19	2.21	> 0.05	
Residual	32	1.90			

G. JANUARY 1984 - QUADRATS. Data were untransformed, and Cochran's test was not significant, $P > 0.05$. $n = 3$ quadrats.

SOURCE	DF	MS	F	P	P'
Species	1	130.02	32.75	< 0.005	< 0.001
Microhabitat	1	808.52	48.21	< 0.001	
SPxMH	1	379.69	95.64	< 0.001	< 0.001
SU(MH)	6	16.77	5.01	< 0.005	
SPxSU(MH)	6	3.97	1.19	> 0.25	
Residual	32	3.35			

Appendix 3

Appendix 3.3. Analyses of variance of distributional data from censuses of microhabitats (mounds and flats) at Woolooware Bay West and Woolooware Bay East. SU = Sampling Unit (see text for definition). Factors were re-tested against the residual in all analyses indicating that this was justified (i.e. when full-model denominators, SU and/or SPxSU, were not significant, $P > 0.25$); the P'-values correspond to tests against the residual.

A. OCTOBER 1985 - TRAPS. Data were transformed to ln (x+1), and Cochran's test was not significant, $P > 0.05$. $n = 3$ traps.

SOURCE	DF	MS	F	P	P'
Mangrove	1	0.74	4.63	> 0.05	< 0.05
Species	1	0.33	0.97	> 0.25	
Microhabitat	1	0.49	3.06	> 0.10	> 0.05
MAxSP	1	1.44	4.24	> 0.05	
MAxMH	1	0.02	0.13	> 0.50	> 0.50
SPxMH	1	2.21	6.50	< 0.025	
MAxSPxMH	1	0.49	1.44	> 0.10	
SU(MAxMH)	12	0.16	0.94	> 0.50	
SPxSU(MAxMH)	12	0.34	2.00	< 0.05	
Residual	64	0.17			

B. OCTOBER 1985 - QUADRATS. Data were transformed to ln (x+1), and Cochran's test was not significant, $P > 0.05$. $n = 3$ quadrats.

SOURCE	DF	MS	F	P	P'
Mangrove	1	1.87	8.90	< 0.025	< 0.005
Species	1	7.42	41.22	< 0.001	< 0.001
Microhabitat	1	25.95	123.57	< 0.001	< 0.001
MAxSP	1	0	0	> 0.50	> 0.50
MAxMH	1	0	0	> 0.50	> 0.50
SPxMH	1	23.83	132.39	< 0.001	< 0.001
MAxSPxMH	1	1.05	5.83	< 0.05	< 0.025
SU(MAxMH)	12	0.21	1.11	> 0.25	
SPxSU(MAxMH)	12	0.18	0.95		
Residual	64	0.19			

Appendix 3.3. (Cont'd.)

C. MARCH 1986 - TRAPS. Data were transformed to ln (x+1), and Cochran's test was not significant, $P > 0.05$. $n = 3$ traps.

SOURCE	DF	MS	F	P	P'
Mangrove	1	0.01	0.05	> 0.50	
Species	1	0.79	4.94	< 0.05	< 0.025
Microhabitat	1	1.19	7.44	< 0.025	
MAxSP	1	0.44	2.10	> 0.10	> 0.05
MAxMH	1	0.07	0.33	> 0.50	
SPxMH	1	3.41	21.31	< 0.001	< 0.001
MAxSPxMH	1	0	0	> 0.50	
SU(MAxMH)	12	0.21	1.50	> 0.10	
SPxSU(MAxMH)	12	0.16	1.14	> 0.25	
Residual	64	0.14			

D. MARCH 1986 - QUADRATS. Data were transformed to ln (x+1), and Cochran's test was not significant, $P > 0.05$. $n = 3$ quadrats.

SOURCE	DF	MS	F	P	P'
Mangrove	1	0.55	1.90	> 0.10	
Species	1	4.43	29.53	< 0.001	< 0.001
Microhabitat	1	34.14	117.72	< 0.001	
MAxSP	1	1.11	7.40	< 0.025	< 0.01
MAxMH	1	0.14	0.48	> 0.50	
SPxMH	1	27.82	185.47	< 0.001	< 0.001
MAxSPxMH	1	0.47	3.13	> 0.10	> 0.05
SU(MAxMH)	12	0.29	2.08	< 0.05	
SPxSU(MAxMH)	12	0.15	1.07	> 0.25	
Residual	64	0.14			

Appendix 3.4. Analysis of variance of the proportion of female *P. laevis* per sampling effort at Woolooware Bay West. Data were untransformed, and Cochran's test was not significant, $P > 0.05$; n = 2 Days, 5 traps per day.

SOURCE	DF	MS	F	P
Season	3	0.12	6.00	< 0.01
Zone	2	0.13	6.50	< 0.025
SxZ	6	0.01	0.50	> 0.05
Residual	12	0.02		

Mean proportion (+ S.E.) of female *P. laevis* per sampling effort in each zone at Woolooware Bay West. n = 2 Days, 5 traps per day.

	TIDAL ZONE			
SEASON & CENSUS	SEAWARD ZONE(A)	MIDMANGROVE ZONE(B)	LANDWARD ZONE(C)	SNK TESTS ON ZONES (P = 0.05)
AUTUMN (AU) (May 1983)	0.51 (0.18)	0.61 (0.11)	0.79 (0.22)	A = B = C
WINTER (WI) (July 1983)	0.25 (0.03)	0.20 (0.14)	0.54 (0.04)	A = B = C
SPRING (SP) (Oct. 1983)	0.38 (0.00)	0.27 (0.06)	0.43 (0.11)	A = B = C
SUMMER (SU) (Jan. 1984)	0.29 (0.11)	0.35 (0.08)	0.55 (0.05)	A = B = C
SNK TESTS ON SEASONS (P = 0.05)	WI=SU=SP=AU	WI=SP=SU=AU	SP=SU=WI=AU	

Appendix 5

APPENDICES TO CHAPTER 5: MECHANISMS UNDERLYING DISTRIBUTIONS

Appendix 5.1. Analyses of variance of the proportions of crabs and their burrows in 3 kinds of mounds versus undisturbed flats and mounds in enclosures of the experiments on topography and composition of the substratum (= material). In each analysis, data were untransformed and Cochran's test was not significant (*P* > 0.05). Means and SNK tests associated with these analyses appear in Tables 5.5 and 5.7. *n* = 3 enclosures. F1 = composition of the half of the enclosure opposite the undisturbed flat half; F2 = topography of the half of the enclosure opposite the undisturbed flat half.

H. cordiformis

		CRABS			BURROWS		
SOURCE	DF	MS	F	*P*	MS	F	*P*
Compos. of mound (F1)	2	0.46	46.00	< 0.001	0.08	8.00	< 0.01
Contrasted with (F2)	1	0.25	25.00	< 0.001	0.16	16.00	< 0.005
F1 x F2	2	0.02	2.00	> 0.10	0.003	0.30	> 0.50
Residual	12	0.01			0.01		

P. laevis

		CRABS			BURROWS		
SOURCE	DF	MS	F	*P*	MS	F	*P*
Compos. of mound (F1)	2	0.31	3.10	> 0.05	0.02	1.00	> 0.25
Contrasted with (F2)	1	0.21	2.21	> 0.10	0.13	6.50	< 0.05
F1 x F2	2	0.01	0.10	> 0.50	0.06	3.00	> 0.05
Residual	12	0.10			0.02		

Appendix 5.2. Analyses of variance of the proportions of crabs and their burrows in undisturbed flats versus mounds and flats in enclosures of the experiment on topography and composition of the substratum (= material). In each analysis, data were untransformed and Cochran's test was not significant ($P > 0.05$). Means and SNK tests associated with these analyses appear in Tables 5.6 and 5.8. $n = 3$ enclosures. F1 = composition of the half of the enclosure opposite the undisturbed flat half; F2 = topography of the half of the enclosure opposite the undisturbed flat half.

H. cordiformis

		CRABS			BURROWS		
SOURCE	DF	MS	F	*P*	MS	F	*P*
Composition (F1)	2	0.18	18.00	< 0.001	0.03	3.00	> 0.05
Topography (F2)	1	0.001	0.10	> 0.50	0.04	4.00	> 0.05
F1 x F2	2	0.23	23.00	< 0.001	0.03	3.00	> 0.05
Residual	12	0.01			0.01		

P. laevis

		CRABS			BURROWS		
SOURCE	DF	MS	F	*P*	MS	F	*P*
Composition (F1)	2	0.17	2.43	> 0.10	0.02	2.00	> 0.10
Topography (F2)	1	0.06	0.86	> 0.25	0.11	11.00	< 0.01
F1 x F2	2	0.08	1.14	> 0.25	0.06	6.00	< 0.025
Residual	12	0.07			0.01		

Appendix 6

APPENDIX TO CHAPTER 6: SUMMARY OF WARREN AND UNDERWOOD 1986, 'THE EFFECTS OF BURROWING CRABS ON THE TOPOGRAPHY OF MANGROVE SWAMPS'

APPENDIX 6.1

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Effects of burrowing crabs on the topography of mangrove swamps in New South Wales

Janice H. Warren and A.J. Underwood
Institute of Marine Ecology, Zoology Building, University of Sydney, Sydney, N.S.W. 2006, Australia

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Abstract: The topography of mangrove swamps near Sydney, Australia, consists of well-drained mounds and poorly-drained flats between mounds. Of several species of crabs abundant in these swamps, the ocypodid *Heloecius cordiformis* (Milne Edwards) burrows most frequently in mounds. When *H. cordiformis* burrow, they deposit excavated material near the entrance to their burrows; the accretion of this material may form mounds. Therefore, not only does microhabitat affect the distribution of crabs, but crabs may affect the topography of the substratum.

To test this proposition, *H. cordiformis* were enclosed in completely flat areas and, during the subsequent four months, the topography of these enclosed areas was compared with ones not containing crabs. Using photogrammetric techniques, the proportion of substratum at several levels of contouring (i.e. the proportion of substratum at heights of 15, 20, 25 mm, etc.) was found to be significantly greater in enclosures containing crabs than in those without crabs. Thus, by their burrowing activities, crabs contribute significantly to the extent of mounds in their natural habitat. Their effects on the distribution of grain-sizes and the abundance of organic material and algae were also investigated. Where crabs were burrowing, there were greater proportions of large particles in the sediments at the surface, and a smaller percentage cover of algae than in enclosures without crabs. Thus, crabs clearly modified their habitat in important ways, and were able to create much of the visible topographic structure in the mangrove swamp.

Key words: *Heloecius cordiformis*; Mangrove-swamp; Crabs; Burrows; Topography; Photogrammetry

INTRODUCTION

The fauna associated with soft substrata has an intimate relationship with the surrounding sediment. The animals ingest the sediment, or food adhered to it, they burrow in it and move through it, and modify it in many physical and chemical ways (for a review, see Dayton, 1984). The relationships between animals and the soft sediments they live on or in have been examined from two perspectives: the effects of the substratum on the animal and the effects of the animal on the substratum. These topics have been reviewed extensively, for example by Carriker (1967) for estuaries, by Rhoads (1974) for the sea floor down to 60 m, by Daiber (1977) for salt marshes and by Jones (1984) and Plaziat (1984) for mangroves.

A subset of these studies has concerned interactions between the substratum and a variety of small, burrowing crabs. Most of these studies have been on the factors affecting the apparent zonal distribution of ocypodid and grapsid crabs, and have considered such variables as particle size, depth to the water table, redox potential, concentration of organic matter, salinity, vegetative cover, and sediment stability (Teal, 1958; Miller, 1961; Ono, 1962; Hartnoll, 1965; Macnae, 1968; Griffin, 1971; Allen & Curran, 1974; Hyatt & Salmon, 1978; Wells, 1983; and many others). Microhabitats within tidal zones have not often been examined (an exception is Bertness & Miller, 1984), although there have been occasional references to greater-than-average abundances of crabs amongst oysters, on the trunks, aerial roots or branches of trees, under pieces of debris, etc. (e.g. Jones, 1984; Plaziat, 1984).

The feeding and burrowing activities of crabs are known to increase the drainage and oxidation of the soil, increase the rate of decomposition of plant debris within the sediments, and can decrease or increase meiofaunal abundances (Bell *et al.*, 1978; Valiela *et al.*, 1978; Montague, 1980, 1982; Howarth & Hobbie, 1982; Hoffman *et al.*, 1984; Bertness, 1985). These activities lead to increased productivity of vegetation, such as the cordgrass *Spartina alterniflora* in salt marshes (Montague, 1982; Bertness, 1985).

In mangrove swamps near Sydney, Australia, two very different microhabitats are interspersed: mound and flats. Mounds are well-drained accumulations of sediment, 0.25–0.50 m^2 in area and up to 100 mm high, although the lower limit for discrimination between "mounds" and "flats" has been somewhat subjective. The surrounding flats are either very wet or submerged during low tide. Mounds generally have a coarser appearance than flats, reflecting a greater proportion of sands as opposed to silts and clays.

The most conspicuous species of crab on the surface is an ocypodid, *Heloecius cordiformis* (Milne Edwards) (Griffin, 1971; Yates, 1978). The crabs excavate burrows to a maximal depth of 40 cm (although most are <25 cm deep). These burrows are simple blind-ending tubes with a single entrance; the entrances are characteristically shaped and unambiguously identifiable as having been made by this species. A significantly greater number of burrows can be found in mounds than on nearby flat surfaces; mean number per 50 × 50 cm quadrat in mounds was 28.5 (SE 2.7) and in flats was 8.8 (SE 1.1) sampled in 22 quadrats during autumn 1983 and summer 1984 in the site studied. When feeding, the crabs spend most of their time within a few cm of the entrances to their burrows. Most feeding is, therefore, on the surfaces of mounds, although crabs sometimes wander into flat areas and can occasionally be observed feeding there. Before being submersed by the incoming tide, and within 2 h of dusk, each crab seals its burrow with a plug of sediment and remains in its burrow throughout high tide and also during the night. The majority of its activities during diurnal low tides are associated with feeding and the maintenance of the burrow.

Like their relatives the fiddler crabs, *H. cordiformis* feed by sifting through the top 3–5 mm of substratum, ingesting detritus, algae and microorganisms on or within the sediments, and ejecting a pellet of sand mixed with mucus (see Miller, 1961; Fielder, 1970; Crane, 1975, for details of the extraction of food and formation of pellets by fiddler crabs). It, therefore, appeared that the feeding and burrowing activities of *H. cordiformis* might alter the composition, distribution of grain-sizes, and the patterns of drainage of the substratum and thus influence the very existence and extent of the mounds themselves. In this paper, we describe the results of experimental tests of this proposal.

MATERIALS AND METHODS

SITE STUDIED AND EXPERIMENTAL ENCLOSURES

To test the effects of *H. cordiformis* on the substratum, 20 initially flat areas (≈ 0.50 m^2 each) were enclosed within circular Formica barriers in the mangrove swamp at Careel Bay, Pittwater, 30 km north of Sydney. For a description of the basic geomorphology and hydrology of this area, see Hutchings & Recher (1974). In the site studied during the year before the experiment, the natural mean density of *H. cordiformis* varied from season to season; seasonal sampling gave mean densities of 26.6 crabs per 0.50 m^2 (SE 2.0, $n = 18$ quadrats) in mounds and only 3.4 crabs per 0.50 m^2 (SE = 1.0, $n = 18$ quadrats) in flat habitats. The site studied was approximately half-way from the front to the back of the swamp and was submersed twice daily by the tide. Barriers were 210–240 cm in circumference, and were 30 cm high. They were buried to a depth of 10–15 cm to prevent crabs from burrowing into or out of the enclosed experimental plots. Solid barriers were used because of the great difficulty of burying mesh fences below the surface of mud full of tangled roots and peg-roots. Several holes (5 mm diameter) were drilled through the barriers to allow rapid drainage of water as the tide fell. Each enclosure was covered with nylon fly-screen (1 mm mesh) to prevent non-experimental crabs from entering and experimental crabs from leaving enclosures.

Sites were chosen with few or no burrows initially in them, and the residents were removed by hand during a 2-wk period before the start of the experiment (23 November 1984). The natural mean density of medium and large *H. cordiformis* (carapace lengths > 10 mm) in the area studied at the start of the experiment was 22.5 per 0.5 m^2 (SE = 1.1, $n = 34$ quadrats). Twenty such crabs (i.e. approximately natural density) were added to 10 randomly-chosen enclosures. No crabs were added to the other enclosures. Crabs used in the experiment were random mixtures of adult males and females, and had carapace lengths of 10–12 mm. A few crabs died during each week of the 5 months that enclosures were in place; these were replaced, as soon as they were discovered, with live crabs of a similar size. Enclosures were inspected every week after the experiment began.

TOPOGRAPHY

The development of topographic features was monitored by photogrammetric procedures. Fourteen and 129 days (7 December 1984 and 1 April 1985, respectively) after crabs were added, stereophotographs were taken of each site with a Wild C-40 camera. On Day 129, stereophotographs were also taken of eight natural mounds and flats 10–15 m from the experimental enclosures. Each of these mounds was surrounded by a white cord at a height below which the substratum would have been considered a "flat". Contour maps drawn from stereophotographs of natural mounds and flats allowed determination of the maximum height of each mound and the mean minimum height of substratum recognizable as a "mound". Although, subjectively, mounds were easily distinguishable from flats, these photographs allowed quantification of this distinction. The contour maps were plotted on a Topocart Analytical Plotter, with an interval of 5 mm in height between contour lines.

Examples of contour maps from experimental enclosures are shown in Fig. 1. Data used to compare topographic complexity between treatments were the proportions of the area inside a barrier that was enclosed by each level of contouring. These areas were measured on a digitizer.

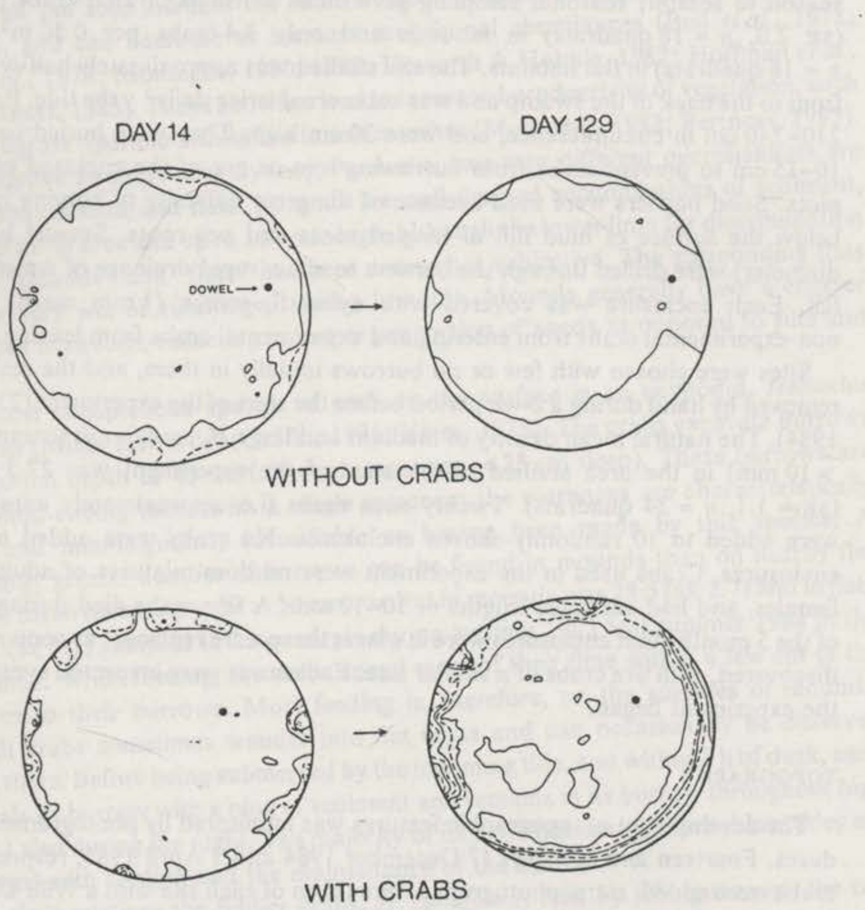

Fig. 1. Contour maps of one enclosure without crabs and one with crabs from stereophotographs taken on Days 14 and 129: in each enclosure, the substratum sloped upwards towards the edge; for simplicity, only the 10-mm contour lines are shown, each enclosing an area of at least that height; a dowel reference peg was placed in each enclosure before the stereophotographs were taken.

SIZES OF PARTICLES IN SEDIMENTS

Three samples of sediment were taken randomly from the edge (i.e. within 5 cm of the surrounding barrier) and three from the centre of each enclosure, 3 wk after the second set of stereophotographs. For each sample, sediment was carefully scraped from the surface of the mud to a depth of 5 mm, until a volume of ≈ 100 ml had been accumulated. Wet samples were filtered through a 2-mm sedimentary sieve to remove twigs, leaves and other large debris. The samples were then put through a 0.063-mm sieve, with ≈ 1.5–2.0 l of tap water, to separate the silts and clays from the sands. The sand fractions retained by the 0.063-mm sieve were dried for 24 h at 80–100 °C, mechanically shaken for 20 min through sieves ranging from 0.063 to 2.00 mm, and weighed (Ingram, 1971). Weights of silts and clays collected after shaking were added to dry weights of silts and clays settling out of solutions from wet-sieving. For comparative purposes, three samples of sediment from each of eight natural mounds and eight flats were also collected, processed and analysed as above.

PROPORTION OF ORGANIC MATTER

To determine whether crabs altered the amount of organic matter in the surface of the substratum, 22-mm diameter cores were sampled to a depth of 20 mm from three random places in enclosures with and without crabs, 3 wk after the second set of stereophotographs. Samples were dried at 80 °C until a stable weight was attained (≈ 12 h) and then the organic matter burned off in a muffle furnace for 7 h at 500 °C, as described by Hirota & Szyper (1975). Oven-dried weights were compared with the ash-free weights to determine the proportion of organic material in the samples.

ABUNDANCE OF ALGAE

Abundance of green algae on the surface of the mud in each enclosure was measured as the percentage of cover using a Perspex quadrat (15 × 15 cm) marked with 100 regularly spaced points; this was tossed haphazardly three times into each enclosure. The number of points over bare sand, fine filamentous algae and thick algae in a mat was recorded. The algal mat consisted of a dense accumulation of filamentous algae, 3–5 mm thick and dark or bright green. Both types of algal cover consisted primarily of mats of micro-algae (mostly pennate diatoms and various unidentified filamentous blue–green algae).

RESULTS

TOPOGRAPHY

In enclosures with *H. cordiformis*, crabs excavated the majority of their burrows within 5 cm of the barriers and, therefore, the substratum in enclosures sloped upward toward the barriers (Fig. 1). This pattern may reflect a response to the presence of the barrier, either to avoid the more open centre of the enclosure, or because of changes in the substratum caused by the barrier. In enclosures without crabs, and just outside all barriers, the substratum also gently sloped upward toward the barriers. This slight increase in height of substratum (typically < 20 mm) was probably an artefact of the barriers.

By Day 14, there was a significantly greater proportion of substratum > 25 mm high in enclosures with crabs than in those without (Fig. 2). By Day 129, the areas enclosed by contour lines 15 mm and higher were significantly greater in sites with crabs (one-factor analyses of variance for each level of contouring in Fig. 2, $P < 0.05$; one enclosure with, and one without were omitted from analyses because the stereo-photographs were lost).

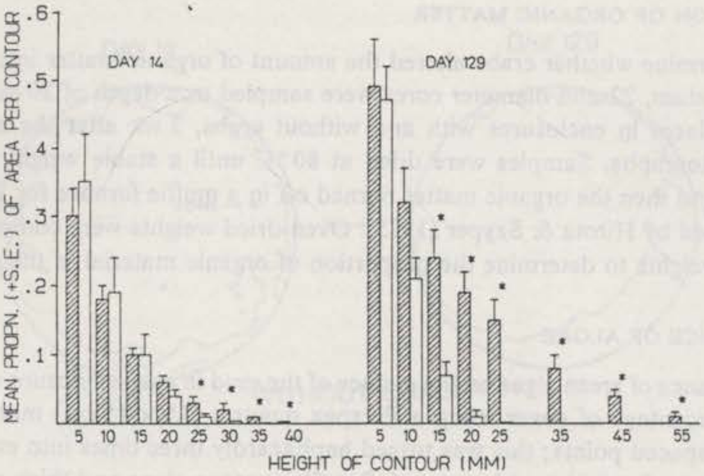

Fig. 2. Mean proportion (+ SE) of area at each level of contouring in enclosures with and without crabs: asterisks denote significant results ($P < 0.05$) of one-factor analyses of variance ($n = 9$ replicate enclosures with (▨) and without (□) crabs).

No formal statistical procedure can be used to compare the data from the two periods of sampling (they are not independent). Nevertheless, two trends can be discerned in Fig. 2. First, the heights of contours in enclosures increased from Day 14 to Day 129 (to 55 mm from ≈40). Secondly, from Day 14 to Day 129 there were large increases in proportions of the surface enclosed by contours equal to or higher than 15 mm – but only where crabs were present. The activities of crabs clearly created, maintained, and continued to enhance the topographic complexity ("moundedness") of the substrata inside enclosures. No such changes occurred inside enclosures without crabs.

The maximum height of eight natural mounds was significantly greater than the highest peak in enclosures with crabs. The highest peaks of enclosures with crabs were, however, significantly greater than the highest peaks in enclosures without crabs (analysis of variance and Student–Newman–Keuls tests, $P < 0.001$; Table I).

Naturally-occurring mounds and flats were sampled by stereophotographs to determine an objective description to allow proper discrimination between these two habitats. The minimum height of the areas sampled because they appeared to be mounds had a mean of 26 mm, with a range of 14–43 mm (compared with zero reference height for areas chosen because they were, subjectively, "flats"). In practice, therefore, any area higher than 14 mm from the surrounding substratum can be reliably defined as a mound.

TABLE I

Mean maximum heights (mm; ± SE) of eight naturally-occurring mounds and highest peak in experimental enclosures by Day 129 ($n = 8$ with and 8 without crabs).

Sample	Mean maximum height
Natural mounds	71.3 (4.0)
Enclosures with crabs	55.[illegible] (2.6)
Enclosures without crabs	21.9 (1.6)

DISTRIBUTION OF GRAIN-SIZES IN SEDIMENTS

Crabs reduced the proportion of fine sediments (silts and clays) in the first 3–5 mm of substratum (Fig. 3). This pattern was observed in samples taken from the edge and from the centre of enclosures, although substratum from the latter had a significantly

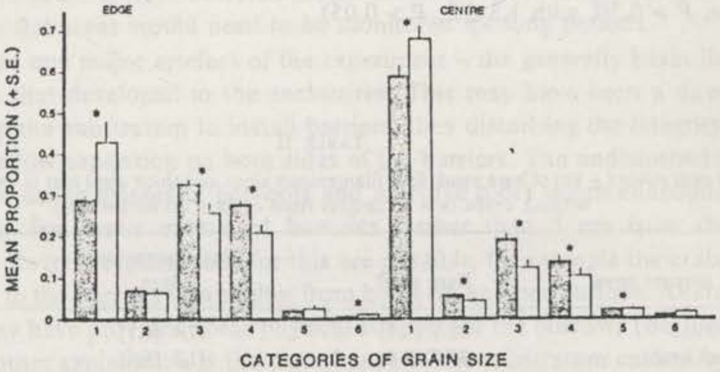

Fig. 3. Mean proportion (+ SE) of grain-sizes in samples of substratum from the edge (within 5 cm of the barrier) and centre (closer to the middle than this) of enclosures with (▨) and without (☐) crabs: asterisks denote significant results ($P < 0.05$) of Kolmogorov–Smirnoff tests (n = 15 replicate samples pooled from 5 enclosures); categories of grain-size are: 1, silts and clays, <0.063 mm; 2, very fine sand, 0.063–0.11 mm; 3, fine sand, 0.11–0.25 mm; 4, medium sand, 0.25–0.50 mm; 5, coarse sand, 0.50–1.00 mm; 6, very coarse sand, 1.00–2.00 mm.

greater proportion of silts and clays. Natural mounds also had significantly less silt and clay than the surrounding flats (Fig. 4). The distribution of grain-sizes was, therefore, similar to that in the enclosures and probably resulted from the natural activities of the unmanipulated population of *H. cordiformis*.

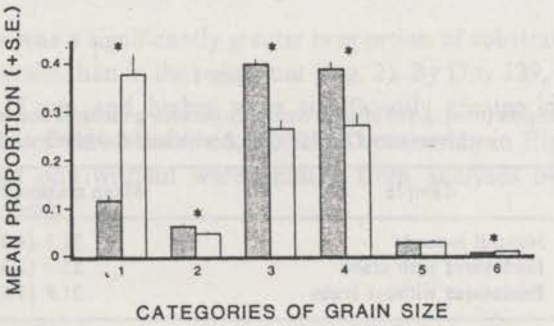

Fig. 4. Mean proportion (+ SE) of grain-sizes in samples of substratum from naturally-occurring mounds (▨) and flats (☐) (n = 8 replicate samples): categories of grain-sizes are as in Fig. 3.

ABUNDANCE OF ORGANIC MATTER AND ALGAE

Although there was slightly more organic matter in samples from the top 20 mm of substratum in enclosures with crabs than those without (means of 0.14 and 0.13 proportions by weight, respectively), the difference was not significant (analysis of variance, $F = 0.30$, with 1,8 d.f., $P > 0.05$).

TABLE II

Mean per cent cover (± SE) of bare sand, fine, filamentous algae and thick algal mat in enclosures with and without crabs (n = 3 samples from each of 10 enclosures).

A. Mean percent cover	Bare sand	Fine, filamentous algae	Thick algal mat
With crabs	82.1 (6.1)	17.4 (6.1)	0.5 (0.5)
Without crabs	33.8 (9.6)	41.3 (6.4)	24.8 (6.9)

		Fine, filamentous algae			Thick algal mat		
B. Analyses of variance	d.f.	M.S.	F-ratio	P	M.S.	F-ratio	P
Source of variation							
Plus versus Minus crabs	1	8,568	7.4	<0.025	8,857	12.5	<0.005
Enclosures (Treatments)	18	1,158	2.1	<0.025	710	2.3	<0.025
Residual	40	545	–		306	–	

Percentage of cover of algae was significantly greater in enclosures without than enclosures with crabs, even though there was considerable (and significant) variation among replicate enclosures (Table II). There was a greater cover of both fine, filamentous and thick mats of algae where crabs had not been placed in enclosures.

DISCUSSION

These experiments unambiguously revealed that crabs form mounds in enclosures and thus influenced the topography of the substratum in a mangrove swamp. Despite problems with artefacts caused by the experimental enclosures, crabs made a considerable difference to the topography of the substratum, which was not matched by processes such as sedimentation in control enclosures without crabs. Interestingly, there was close correspondence between the minimum height that could be identified as defining a mound (14 mm) and the heights of topographic contours that were affected by crabs (≥ 15 mm; see Fig. 2). Thus, significantly more topographic relief at heights of 15 mm and greater was found in enclosures with crabs than in those without. These heights correspond with the minimal heights of natural mounds in the swamp.

The mounds in experimental enclosures did not, however, reach the greatest heights of the eight natural mounds that were also photographed. The simplest explanation for this is that the mounds in enclosures were the product of only 20 crabs for 129 days. Natural mounds may have been built and maintained by a larger number than this. Although 20 crabs per 0.50 m^2 was about the mean density in the site studied, as many as 40 crabs per 0.50 m^2 are not uncommon in some areas (unpubl. data). Natural mounds were probably older than those in enclosures, which were built in <4 months, and would, therefore, have accreted more sediment. To investigate this, new burrows in naturally flat areas would need to be monitored for long periods.

There was one major artefact of the experiment – the generally basin-like shape of substratum that developed in the enclosures. This may have been a direct result of breaking up the substratum to install barriers, thus disturbing the integrity of the soil enough to allow expansion on both sides of the barriers. The undisturbed substratum consisted of dense masses of pegroots and nutritive roots which consolidate the soil.

Relatively few crabs excavated burrows further than 5 cm from the edges of enclosures. Several explanations for this are possible, for example the crabs may have responded to the barriers as a shelter from being on an open surface. Alternatively, the barriers may have provided some physical support for the burrows (Bertness & Miller, 1984). Another explanation is the disturbance of the substratum caused by the installation of the barriers (see above); crabs may have found it easier to excavate burrows in such disturbed sediments. Further work is needed to distinguish among such alternative explanations.

The greater proportion of sands in areas where crabs burrowed could have resulted from the crabs depositing coarse material from beneath the surface as they excavated and maintained their burrows (thus covering the typically fine sediments on the surface of flats). Alternatively, coarser sediments might have been exposed by the removal of silts and clays when *H. cordiformis* transferred large balls of moist sediment from flats into their burrows before inundation by the tide (Fielder, 1970). During one period of low tide, a single crab can take as many as 20–30 of these balls down its burrow. The composition of sediments in these balls warrants further investigation. The relative importance of burial of fine sediment under coarser, excavated material versus the removal of fine material has not been examined here, but could be tested by covering the surface with a fine layer of sediment of a different colour or composition of minerals and later determining if such material had disappeared (down burrows) or had merely been covered with coarser material.

The only other study (besides the present) that has quantitatively examined the effect of crabs on the distribution of grain-sizes of the substratum was that of Hoffman *et al.* (1984) on the mud fiddler crab, *Uca pugnax*. They found no significant effects of the crabs on the sorting and size-frequency of particles in the surface of enclosures with and without crabs, in contrast to the marked effects described here. It is, however, probable that their samples of sediment (the top 20 mm and from 50–100 mm below the surface of the mud) were too deep for any effects of feeding to be demonstrable. With respect to feeding by the crabs, the only relevant layer of the substratum is the top few millimetres – the depth to which crabs feed (see Miller, 1961; Fielder, 1970; Crane, 1975). Where surface sediments are sampled to depths greater than a few millimetres, the sizes of particles in the surface layers would be "swamped" by the deeper material (that would be unaffected by the presence or absence of crabs feeding on the surface). Below a thin layer at the surface, the distribution of sizes of particles could be affected by burrowing activities of the crabs (as discussed above); this is not relevant to our examination of the surface layers themselves.

Because many crabs consume detritus and algae as they scrape up the first few millimetres of substratum (Miller, 1961; Crane, 1975), it was expected that enclosures with crabs would have a smaller proportion of organic material than enclosures without crabs. The results did not support this prediction. The simplest explanation for the lack of effect of crabs on the organic content of surface sediments is that just discussed – that the cores for analysis of organic content of the sediments may have been too deep (20 mm) to allow detection of differences in the surface layer of the substratum (i.e. the top few millimetres). In the present study, the samples were not taken with this requirement in mind, and some difficulty was experienced with attempts to sample only the shallowest layers accurately.

Nevertheless, there are other processes that could explain how the presence of crabs makes no difference to the organic content of the mud. Although this has not been examined, *Heloecius cordiformis* may be "gardening" microorganisms by providing inorganic nutrients or increasing the penetration of oxygen into the substratum as the crabs sift through the sediments at the surface. Crabs may be depositing organic matter from their burrows onto the surface of the substratum (Montague, 1980). Mastication of organic material, or the movements of the crabs may increase the available surface area for microbial activity (Gosselink & Kirby, 1974; Hoffman *et al.*, 1984).

If harvesting by *H. cordiformis* were inefficient, its feeding activities would not be expected to reduce the abundance of microorganisms or organic matter. Robertson *et al.* (1980) showed that *Uca pugilator*, a sand-dwelling species, had a harvesting efficiency of 42% and an extraction efficiency of 90%, leaving 62% of the available food (microorganisms and detritus) in the sediment. This was calculated to represent only a 10% reduction of the daily microbial production in the sediment from the feeding activity of *Uca* (Jones, 1984). Alternatively, if the natural rate of productivity were very great, any effect by crabs might be relatively small and therefore difficult to detect.

The direct estimate of algal abundance demonstrated a significantly greater cover of microalgae in enclosures without crabs. These results do not support the suggestions by Montague (1980) that mechanical disturbance of the surface by the feeding activities of fiddler crabs stimulates algal growth.

The effect of *Heloecius cordiformis* on the topography of mangrove swamps was examined for only the middle 4 months of their 8- to 9-month period of activity on the surface of the substratum (spring through autumn). During winter, *H. cordiformis* in local mangrove swamps are rarely seen out of the burrow, although Macnae (1968) suggested that these crabs might emerge from their burrows every few days to feed. Without continued deposition of material from burrows onto the surface, tides and heavy rains might be expected to erode at least some proportion of mounds. Approximately 180 burrows were marked with small, wooden sticks and these (and the mounds they were in) were found to persist over winter.

From the present experiments, crabs clearly influenced the abundance of algae, the distribution of particle-sizes and the topographic complexity of the substratum in mangrove swamps. Such effects can potentially persist for long periods. This study has demonstrated that the structure of suitable habitats for crabs in mangrove swamps is a complex function of the activities of the animals and not simply a result of physical features of the environment.

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REFERENCES

ALLEN, E.A. & H.A. CURRAN, 1974. Biogenic sedimentary structures produced by crabs in lagoon margin and salt marsh environments near Beaufort, North Carolina. *J. Sed. Petrol.*, Vol. 44, pp. 538–548.

BELL, S.S., M.C. WATZIN & B.C. COULL, 1978. Biogenic structure and its effect on the spatial heterogeneity of meiofauna in a salt marsh. *J. Exp. Mar. Biol. Ecol.*, Vol. 35, pp. 99–107.

BERTNESS, M.D., 1985. Fiddler crab regulation of *Spartina alterniflora* production on a New England salt marsh. *Ecology*, Vol. 66, pp. 1042–1055.

BERTNESS, M.D. & T. MILLER, 1984. The distribution and dynamics of *Uca pugnax* (Smith) burrows in a New England salt marsh. *J. Exp. Mar. Biol. Ecol.*, Vol. 83, pp. 211–237.

CARRIKER, M.R., 1967. Ecology of estuarine benthic invertebrates: a perspective. In, *Estuaries*, edited by G.H. Lauff, Am. Assoc. Adv. Sci. Publication No. 83, Washington, D.C., pp. 442–487.

CRANE, J., 1975. *Fiddler crabs of the world – Ocypodidae: genus* Uca. *Part II: toward an evolutionary synthesis.* Princeton University Press, New Jersey, 736 pp.

DAIBER, F.C., 1977. Salt-marsh animals: distributions related to tidal flooding, salinity and vegetation. In, *Ecosystems of the world. Volume I. Wet coastal ecosystems*, edited by V.J. Chapman, Elsevier, Amsterdam, pp. 79–108.

DAYTON, P.K., 1984. Processes structuring some marine communities: are they general? In, *Ecological communities: conceptual issues and the evidence*, edited by D.R. Strong *et al.*, Princeton University Press, New Jersey, pp. 181–197.

FIELDER, D.R., 1970. The feeding behaviour of the sand crab *Scopimera inflata* (Decapoda, Ocypodidae). *J. Zool.*, Vol. 160, pp. 35–49.

GOSSELINK, J.G. & C.J. KIRBY, 1974. Decomposition of salt marsh grass, *Spartina alterniflora* Loisel. *Limnol. Oceanogr.*, Vol. 19, pp. 825–832.

GRIFFIN, D.J.G., 1971. The ecological distribution and behaviour of ocypodid shore crabs (Crustacea : Brachyura) in Tasmania. *J. Anim. Ecol.*, Vol. 40, pp. 597–621.

HARTNOLL, R.G., 1965. Notes on the marine grapsid crabs of Jamaica. *Proc. Linn. Soc. London*, Vol. 176, pp. 113–147.

HIROTA, J. & J.P. SZYPER, 1975. Separation of total particulate carbon into inorganic and organic components. *Limnol. Oceanogr.*, Vol. 20, pp. 896–900.

HOFFMAN, J.A., J. KATZ & M.D. BERTNESS, 1984. Fiddler crab deposit-feeding and meiofaunal abundance in salt marsh habitats. *J. Exp. Mar. Biol. Ecol.*, Vol. 82, pp. 161–174.

HOWARTH, R.W. & J.E. HOBBIE, 1982. The regulation of decomposition and heterotrophic microbial activity in salt marsh soils: a review. In, *Estuarine comparisons*, edited by V.S. Kennedy, Academic Press, New York, pp. 183–207.

HUTCHINGS, P.A. & H.F. RECHER, 1974. The fauna of Careel Bay with comments on the ecology of mangrove and sea-grass communities. *Aust. Zool.*, Vol. 18, pp. 99–128.

HYATT, G.W. & M. SALMON, 1978. Combat in the fiddler crabs *Uca pugilator* and *U. pugnax*: a quantitative analysis. *Behaviour*, Vol. 65, pp. 182–211.

INGRAM, R.L., 1971. Sieve analysis. In, *Procedures in sedimentary petrology*, edited by R.E. Carver, Wiley-Interscience, New York, pp. 49–67.

JONES, D.A., 1984. Crabs of the mangal ecosystem. In, *Hydrobiology of the mangal*, edited by F.D. Por & I. Dor, W. Junk Publishers, The Hague, pp. 89–109.

MACNAE, W., 1968. A general account of the fauna and flora of mangrove swamps and forests in the Indo-West Pacific region. *Adv. Mar. Biol.*, Vol. 6, pp. 78–270.

MILLER, D.C., 1961. The feeding mechanism of fiddler crabs with ecological considerations of feeding adaptations. *Zoologica*, Vol. 46, pp. 89–100.

MONTAGUE, C.L., 1980. A natural history of temperate western Atlantic fiddler crabs (genus *Uca*) with reference to their impact on the salt marsh. *Contrib. Mar. Sci.*, Vol. 23, pp. 25–55.

MONTAGUE, C.L., 1982. The influence of fiddler crab burrows and burrowing on metabolic processes in saltmarsh sediments. In, *Estuarine comparisons*, edited by V.S. Kennedy, Academic Press, New York, pp. 283–301.

ONO, Y., 1962. On the habitat preference of ocypodid crabs. *Mem. Fac. Sci., Kyushu Univ., Ser. E (Biol.)*, Vol. 3, pp. 143–163.

PLAZIAT, J.C., 1984. Mollusk distribution in the mangal. In, *Hydrobiology of the mangal*, edited by F.D. Por & I. Dor, W. Junk Publishers, The Hague, pp. 111–143.

RHOADS, D.C., 1974. Organism–sediment relations on the muddy sea floor. *Oceanogr. Mar. Biol. Annu. Rev.*, Vol. 12, pp. 263–300.

ROBERTSON, J.R., K. BANCROFT, G. VERMEER & K. PLAISIER, 1980. Experimental studies on the foraging behaviour of the sand fiddler crab *Uca pugilator* (Bosc 1802). *J. Exp. Mar. Biol. Ecol.*, Vol. 44, pp. 67–83.

TEAL, J.M., 1958. Distribution of fiddler crabs in Georgia salt marshes. *Ecology*, Vol. 39, pp. 185–193.

VALIELA, I., J.M. TEAL & W.G. DEUSER, 1978. The nature of growth forms in the salt marsh grass, *Spartina alterniflora*. *Am. Nat.*, Vol. 112, pp. 461–470.

WELLS, A.G, 1983. Distribution of mangrove species in Australia. In, *Biology and ecology of Australian mangroves*, edited by H.J. Teas, W. Junk Publishers, The Hague, pp. 57–76.

YATES, R.W., 1978. Aspects of the ecology and reproductive biology of crabs in a mangrove swamp at Patonga, New South Wales. M.Sc. thesis, University of Sydney, Australia, 135 pp.

Appendix 7

APPENDICES TO CHAPTER 7: BEHAVIOURAL ASPECTS OF THE ECOLOGY OF *H. CORDIFORMIS*

Appendix 7

Appendix 7.1. Analyses of variance of the proportion of time spent in 4 common behaviours recorded by direct observation and videotaping. Data are from the landward zone during the early and middle periods of activity on 4 days in May 1986. Sexes have been pooled. For each analysis, data were untransformed, and Cochran's test was not significant ($P > 0.05$); $n = 3$ crabs.

A. Feeding and Maintenance of Burrows.

SOURCE	DF	MS	F	P
Method	1	0.09	9.00	> 0.10
Period	1	0.05	0.42	> 0.50
Day (Method)	2	0.01	0.25	> 0.50
Behaviour	1	2.67	29.67	< 0.05
M x P	1	0.03	0.25	> 0.50
M x B	1	0.02	0.22	> 0.50
P x D	2	0.12	3.00	> 0.05
P x B	1	0.17	2.43	> 0.10
D x B	2	0.09	2.25	> 0.05
M x P x B	1	0.12	1.71	> 0.25
P x D x B	2	0.07	1.75	> 0.10
Residual	32	0.04		

(nb: To provide a more powerful test of Method, the mean square for this factor was tested against that of the residual [because its original denominator, Day, was not significant]. When this was done, method was still not significant, $P > 0.10$.)

B. Pausing and Other Behaviour. (nb: comparison of Pausing with Forming Mud Balls gave similar results).

SOURCE	DF	MS	F	P
Method	1	0.06	0.38	> 0.50
Period	1	0.002	0.20	> 0.50
Day (Method)	2	0.16	8.00	< 0.005
Behaviour	1	0.78	9.75	> 0.05
M x P	1	0.02	2.00	> 0.25
M x B	1	0.04	0.50	> 0.50
P x D	2	0.01	0.50	> 0.25
P x B	1	0.01	0.50	> 0.50
D x B	2	0.08	4.00	< 0.05
M x P x B	1	0.01	0.50	> 0.50
P x D x B	2	0.02	1.00	> 0.25
Residual	32	0.02		

(nb: A more powerful test of method could not be done because day [the denominator specified by the full model to construct the appropriate F-ratio for method] was significant and could not be combined with the residual.)

Appendix 7

Appendix 7.2. Analyses of variance of the proportion of time spent in 4 common behaviours recorded by direct observation and vidotaping. Data are from the landward zone during the early period of activity on 21 and 22 May 1986. Sexes have been pooled; $n = 2$ crabs and S.U. = sampling unit.

A. Feeding and Maintenance of burrows. Data were transformed to arcsin $\sqrt{x}$, and Cochran's test was not significant ($P > 0.05$).

SOURCE	DF	MS	F	P
Method	1	123.12	0.88	> 0.25
S.U. (Method)	2	140.34	0.80	> 0.25
Behaviour	1	4066.10	184.24	< 0.01
M x B	1	97.72	4.43	> 0.10
S.U. x B	2	22.07	0.13	> 0.50
Residual	8	175.09		

A'. Feeding and Maintenance. To provide more powerful tests of method, behaviour and M x B, the sums of squares for sampling unit and S.U. x B were pooled with that of the residual and new F-values calculated.

Method	1	123.12	0.86	> 0.25
Behaviour	1	4066.10	28.28	< 0.001
M x B	1	97.72	0.70	> 0.25
Residual	12	143.80		

B. Pausing and Other Behaviour (nb: Comparison of pausing with forming mud balls gave similar results). Data were untransformed, and Cochran's test was not significant ($P > 0.05$).

SOURCE	DF	MS	F	P
Method	1	0.006	2.00	> 0.25
S.U. (Method)	2	0.003	0.15	> 0.50
Behaviour	1	0.04	2.00	> 0.25
M x B	1	0.02	1.00	> 0.25
S.U. x B	2	0.02	1.00	> 0.25
Residual	8	0.02		

B'. Pausing and Other Behaviour. To provide more powerful tests of method, behaviour, and M x B, the sums of squares for sampling unit and S.U. x B were pooled with that of the residual and new F-values calculated.

Method	1	0.006	0.30	> 0.50
Behaviour	1	0.04	2.00	> 0.10
M x B	1	0.02	1.00	> 0.25
Residual	12	0.02		

Appendix 7.3. Seasonal difference in degree of association between daily and tidal events and the onset and termination of activity of *H. cordiformis* on the surface. Table entries are mean number of minutes (+ S.E.).

A. When onset of activity is limited by lack of daylight (i.e. pre-dawn emersion) and termination is imposed by diurnal submergence:

	EARLY SPRING (OCTOBER 1985)	LATE AUTUMN (MAY/JUNE 1986)
1. Time lag (in minutes) between dawn and onset of activity.	15 (11) *n* = 5 days, Midmangrove Zone	225 (15) *n* = 3 days, Midmangrove Zone
		180 (30) *n* = 3 days, Landward Zone
2. Time (in minutes) not exploited between termination of activity and submergence.	15 (5) *n* = 5 days, Midmangrove Zone	60 (17) *n* = 3 days, Midmangrove Zone
		68 (23) *n* = 4 days, Landward Zone

B. When onset of activity is limited by submergence (i.e. post-dawn emersion) and termination imposed by nightfall:

	EARLY SPRING (OCTOBER 1985)	LATE AUTUMN (MAY/JUNE 1986)
1. Time lag (in minutes) between emersion and onset of activity.	5 (0) *n* = 5 days, Midmangrove Zone	50 (10) *n* = 3 days, Midmangrove Zone
		75 (26) *n* = 3 days, Landward Zone
2. Time (in minutes) *not* exploited between termination of activity and dusk.	8 (46)[1] *n* = 4 days, Midmangrove Zone	75 (15) *n* = 2 days, Midmangrove Zone

[1] Large S.E. because on one day crabs remained active on surface until 1 hour after dusk.

Appendix 7.4. Analyses of variance of the proportion of time spent in 4 common behaviours observed in the landward zone during the earlly and late periods of activity on 4 days in May and June 1986. Sexes have been pooled. *n* = 2 crabs and S.U. = sampling unit.

A. Feeding and Maintenance of Burrows. Data were untransformed, and Cochran's test was not significant (*P* > 0.05).

SOURCE	DF	MS	F	P
Period	1	0.15	1.36	> 0.25
Day (Period)	2	0.11	5.50	> 0.05
S.U. (Day)	4	0.02	0.33	> 0.50
Behaviour	1	1.94	14.92	> 0.05
P x B	1	0.26	2.00	> 0.25
D x B	2	0.13	6.50	> 0.05
S.U. x B	4	0.02	0.33	> 0.50
Residual	16	0.06		

A'. Feeding and Maintenance of Burrows. For more powerful tests of period and behaviour, the mean squares for these factors were compared with that of the residual (without pooling of sums of squares).

Period	1	0.15	2.50	> 0.10
Day (Period)	2	0.11	1.83	> 0.10
S.U.(Day)	4	0.02	0.33	> 0.50
Behaviour	1	1.94	32.33	< 0.001
P x B	1	0.26	4.33	> 0.05
D x B	2	0.13	2.17	> 0.25
S.U. x B	4	0.02	0.33	> 0.50
Residual	16	0.06		

Appendix 7.4. (Cont'd.)

B. Pausing and Other Behaviour (nb: Comparison of pausing with forming mud balls gave similar results.) When data were transformed to $\sqrt{x+1}$, Cochran's test was not significant ($P >$ 0.05).

SOURCE	DF	MS	F	P
Period	1	0.16	1.23	> 0.25
Day (Period)	2	0.13	2.60	> 0.10
S.U. (Day)	4	0.05	0.83	> 0.50
Behaviour	10	0.10	0.38	> 0.50
P x B	1	0.01	0.04	> 0.50
D x B	2	0.26	4.33	> 0.05
S.U. x B	4	0.06	1.00	> 0.25
Residual	16	0.06		

B'. Pausing and Other Behaviour. For a more powerful test of period and behaviour, mean squares for these factors were compared with that of the residual (without pooling of sums of squares).

Period	1	0.16	2.67	> 0.10
Day (Period)	2	0.13	2.17	> 0.10
S.U. (Day)	4	0.05	0.83	> 0.50
Behaviour	1	0.10	1.67	> 0.10
P x B	1	0.26	4.33	> 0.05
D x B	2	0.06	1.00	> 0.25
S.U. x B	4	0.06	1.00	> 0.25
Residual	16	0.06		

Appendix 7.5. Analyses of variance of the proportion of time spent in 4 common behaviours observed in the landward zone during the early and middle periods of activity on 21 May 1986; $n = 3$ crabs.

A. Feeding and Maintenance of Burrows. Data were untransformed, and Cochran's test was not significant ($P > 0.05$).

SOURCE	DF	MS	F	P
Period	1	0.04	4.00	> 0.10
S.U. (Period)	2	0.01	0.25	> 0.50
Behaviour	1	1.72	86.00	< 0.025
P x B	1	0.02	1.00	> 0.25
S.U. x B	2	0.02	0.50	> 0.50
Residual	16	0.04		

A'. For a more powerful test of period and behaviour, the mean squares for these factors were compared with that of the residual (without pooling of sums of squares).

Period	1	0.04	1.00	> 0.25
S.U. (Period)	2	0.01	0.25	> 0.50
Behaviour	1	1.72	43.00	< 0.001
P x B	1	0.02	0.50	> 0.50
S.U. x B	2	0.02	0.50	> 0.50
Residual	16	0.04		

B. Pausing and Other Behaviour. (nb: Similar results were found when pausing was compared to forming mud balls). Data were transformed to arcsin $\sqrt{x}$, and Cochran's test was not significant ($P > 0.05$).

SOURCE	DF	MS	F	P
Period	1	1.79	0.05	> 0.50
S.U. (Period)	2	33.41	0.30	> 0.50
Behaviour	1	2124.13	63.58	< 0.025
P x B	1	1.78	0.05	> 0.50
S.U. x B	2	33.41	0.30	> 0.50
Residual	16	112.92		

B'. Pausing and Other Behaviour. For a more powerful test of period and behaviour, the mean squares for these factors were compared with that of the residual (without pooling of sums of squares).

Period	1	1.79	0.01	> 0.50
S.U. (Period)	2	33.41	0.30	> 0.50
Behaviour	1	2124.13	18.81	< 0.001
P x B	1	1.78	0.02	> 0.50
S.U. x B	2	33.41	0.30	> 0.50
Residual	16	112.92		

Appendix 7.6. Summary of observations of the less common behaviours of H. cordiformis.

Over the 5-week period of this study, 16 occurrences of courtship were observed. Of these, only 2 were followed by coupling at the surface. The remaining 14 courtships were terminated when a female rejected a male by pushing him away, waving him off or descending into the burrow. In a single occurrence, a male attempted to couple with a female without first courting her and was rejected by the female. Courtship/coupling was initiated only by males. All but two episodes occurred at a female's burrow; the two exceptions took place 6 cm and 8 cm from the female's burrow. Of 14 courtships/couplings between burrow-owning males and females, 9 involved males courting females in the nearest or next-nearest burrow. The mean distance betwen these burrows was 13.44 cm (SE = 2.14 cm). Only 3 courtships occurred between females owning burrows within the site under observation and males wandering through the site. Courtship and coupling was observed only during the early and middle periods in each zone.

Waving displays, lunges toward another crab, combat and sudden dashes to the burrow were almost always related to defence of the burrow. Exceptions include females 'waving off' courtship attempts by males and dashes to the burrow for refuge (frequently in response to a low-flying bird above the site). All 4 of these behaviours were performed by males and females. Occurrences of these behaviours in May and June 1986 (late autumn) were too infrequent for meaningful statistical analyses to compare males and females.

Of 15 sudden dashes back to a burrow (5 by males and 10 by females), 11 were in response to the approach of a neighbouring burrow-owner and 4 were in response to a wanderer (1 female and 3 male wanderers). Of 25 occurrences of burrow-owning crabs displaying (with the chelae) to other crabs, 1 was by a female toward a neighbouring female, 13 were by females toward 11 resident and 2 wandering males (4 of these were to reject courtship advances), 5 were by males toward 3 resident and 2 wandering males and 6 were by males toward 3 resident and 3 wandering females. Four lunges of one crab toward another were observed. These were done by and instigated by males and females. Of 4 occurrences of combat, one was between a burrow-owning male and a burrow-owning female, 2 were between a burrow-owning male and a wandering female and one was between two burrow-owning males. For the 19 observed interactions involving defence of burrows from other burrow-owners, all were between immediate neighbours (i.e. no intervening burrows), and the mean distance between burrows was 15.26 cm (SE = 1.37 cm).

Appendix 7.7. Mean proportion of time (+ S.E.) spent by H. cordiformis in the burrow after the first emergence. Data are from the analysis of variance in Table 7.8, D, and are presented here untransformed; n = 2 crabs.

	MALES	FEMALES
Early Period	0.37 (0.02)	0.25 (0.14)
Middle Period	0.29 (0.12)	0.11 (0.03)
Late Period	0.10 (0.02)	0.44 (0.11)

Appendix 7.8. Mean proportion of crabs (+ S.E.) making at least one excursion from the burrow during the early period of activity in both zones on 23, 24 and 25 May 1986. Data are from the analysis of variance in Table 7.10; n = 3 sampling units.

Midmangrove Zone:	
Males	1.00 (0)
Females	0.79 (0.07)
Landward Zone:	
Males	1.00 (0)
Females	1.00 (0)

Appendix 7.9. Analysis of variance of the proportion of time spent by crabs at or 1-9 cm away from the burrow in the landward zone, during the early and middle periods of activity on 21 May 1986. Sexes have been pooled. Data were untransformed, and Cochran's test was not significant ($P > 0.05$); n = 3 crabs.

SOURCE	DF	MS	F	P
Period	1	0.01	1.00	> 0.25
S.U.(Period)	2	0.01	0.20	> 0.50
Distance	1	0.40	3.64	> 0.10
P x D	1	0.04	0.36	> 0.50
S.U. x D	2	0.11	2.20	> 0.10
Residual	16	0.05		

(nb: For a more powerful test of Period, the mean square for this factor was compared with that of the residual. When this was done, F = 0.20, $P > 0.50$. Distance and Period x Distance could not be re-tested against the residual because the full-model denominator for each, which was S.U. x D, had a P-value of < 0.25).

Appendix 7.10. Analysis of variance of the proportion of time spent by crabs at or 1-9 cm from the burrow, as determined by direct observation or videotaping (Methods). Data are from the landward zone, during the early and middle periods of activity on 4 days in May 1986. Sexes have been pooled. Data were untransformed, and Cochran's test was not significant ($P > 0.05$); $n = 3$ crabs.

SOURCE	DF	MS	F	P
Method	1	0.01	10.00	> 0.05
Period	1	0.06	6.00	> 0.10
Day(Method)	2	0.001	0.02	> 0.20
Distance	1	0.48	9.60	> 0.05
M x P	1	0.004	0.40	> 0.50
M x Dist	1	0.18	3.60	> 0.10
P x Day	2	0.01	0.20	> 0.50
P x Dist	1	0.25	6.25	> 0.10
Day x Dist	2	0.05	1.00	> 0.25
M x P x Dist	1	0.002	0.05	> 0.50
P x Day x Dist	2	0.04	0.80	> 0.25
Residual	32	0.05		

Factors with original full-model denominators having $P > 0.25$ were re-tested over the residual and gave the following results:

SOURCE	P
Method	> 0.50
Period	> 0.25
M x P	> 0.50
Distance	< 0.005
M x Dist	> 0.05
P x Dist	< 0.05
M x P x Dist	> 0.50

Appendix 7.11. Analysis of variance of the proportion of time crabs spent at or 1-9 cm away from the burrow in the landward zone, during the early and late periods of activity on 4 days in May 1986. Sexes have been pooled. Data were untransformed, and Cochran's test was not significant (*P* > 0.05); *n* = 2 crabs. S.U. = sampling unit.

SOURCE	DF	MS	F	P
Period	1	0.01	0.33	> 0.50
Day(Period)	2	0.03	0.75	> 0.50
S.U.(Day)	4	0.04	1.33	> 0.25
Distance	1	2.49	7.11	> 0.10
P x Dist	1	0.29	0.83	> 0.25
Day x Dist	2	0.35	7.00	< 0.05
S.U. x Dist	4	0.05	1.67	> 0.10
Residual	16	0.03		

nb: More powerful tests of Period and Day (by testing over the residual) also indicated no significant effect of Period (*P* > 0.50) or Day (as a main factor, *P* > 0.25).

REFERENCES

Alheit, J. and E. Naylor, 1976. Behavioural basis of intertidal zonation in *Eurydice pulchra* Leach. J. Exp. Mar. Biol. Ecol. **23**:135-144.

Allen, E.A. and H.A. Curran, 1974. Biogenic sedimentary structures produced by crabs in lagoon margin and salt marsh environments near Beaufort, North Carolina. J. Sed. Petrol. **44**:538-548.

Aller, J.Y. and R.C. Aller, 1986. Evidence for localized enhancement of biological activity associated with tube and burrow structures in deep-sea sediments at the HEBBLE site, western North Atlantic. Deep-Sea Research **33**:755-790.

Aller, R.C. and R.E. Dodge, 1974. Animal-sediment relations in a tropical lagoon Discovery Bay, Jamaica. J. Mar. Res. **32**:209-232.

Ansell, A.D. and A. Trevallion, 1969. Behavioural adaptations of intertidal molluscs from a tropical sandy beach. J. Exp. Mar. Biol. Ecol. **4**:9-35.

Bailey-Brock, J.H., 1979. Sediment trapping by chaetopterid polychaetes on a Hawaiian fringing reef. J. Mar. Res. **37**:643-656.

Barnes, R.S.K., 1981. An experimental study of the pattern and significance of the climbing behaviour of *Hydrobia ulvae* (Pennant). J. Mar. Biol. Ass. U.K. **61**:285-299.

Barnes, R.S.K., 1986. Daily activity rhythms in the intertidal gastropod *Hydrobia ulvae* (Pennant). Estuar. Coast. Shelf Sci. **22**:325-334.

Barnwell, F.H., 1968. The role of rhythmic systems in the adaptation of fiddler crabs to the intertidal zone. Am. Zool. **8**:569-583.

Bell, S.S., M.C. Watzin and B.C. Coull, 1978. Biogenic structure and its effect on the spatial heterogeneity of meiofauna in a salt marsh. J. Exp. Mar. Biol. Ecol. **35**:99-107.

Berry, A.J., 1963. Faunal zonation in mangrove swamps. Bull. Nat. Mus. St. Singapore **32**:90-98.

Berry, A.J., 1972. The natural history of West Malaysian mangrove faunas. Malay. Nat. J. **25**:135-162.

Bertness, M.D., 1985. Fiddler crab regulation of *Spartina alterniflora* production on a New England salt marsh. Ecology **66**:1042-1055.

Bertness, M.D. and T. Miller, 1984. The distribution and dynamics of *Uca pugnax* (Smith) burrows in a New England salt marsh. J. Exp. Mar. Biol. Ecol. **83**:211-237.

References

Boshe, J.I., 1982. Predation of fiddler crabs Uca stenodactyla (Ocypodidae) by the common shore birds in Pangani Beach, Tanzania. Afr. J. Ecol. 20:237-240.

Boucot, A.J., 1981. Principles of Benthic Marine Paleoecology. Academic Press, New York, 463 pp.

Brenchley, G.A., 1981. Disturbance and community structure: an experimental study of bioturbation in marine soft-bottom environments. J. Mar. Res. 39:767-790.

Cameron, A.M., 1966. Some aspects of the behaviour of the soldier crab Mictyris longicarpus. Pac. Sci. 20:224-234.

Chapman, A.R.O., 1973. A critique of prevailing attitudes towards the control of seaweed zonation on the sea shore. Bot. Mar. 16:80-82.

Christy, J.H., 1978. Adaptive significance of reproductive cycles in the fiddler crab Uca pugilator: a hypothesis. Science 199:453-455.

Christy, J.H., 1982a. Adaptive significance of semilunar cycles of larval release in fiddler crabs (genus: Uca): test of an hypothesis. Biol. Bull. 163:251-263.

Christy, J.H., 1982b. Burrow structure and use in the sand fiddler crab, Uca pugilator (Bosc). Anim. Behav. 30:687-694.

Christy, J.H. and M. Salmon, 1984. Ecology and evolution of mating systems of fiddler crabs (genus Uca). Biol. Rev. 59:483-509.

Cogger, H.G., 1979. Reptiles and Amphibians of Australia (Second Edition). A.H. and A.W. Reed, Sydney, 584 pp.

Colby, D.R. and M.S. Fonseca, 1979. Application of probability sampling designs for estimation of density and biomass of Uca pugilator. Ann. Rep. Southeast Fish. Ctr. Beaufort Lab., North Carolina, pp. 307-321.

Connell, J.H., 1972. Community interactions on marine rocky intertidal shores. Ann. Rev. Ecol. Syst. 3:169-192.

Connell, J.H., 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. In, Ecology and Evolution of Communities, edited by M.L. Cody and J.M. Diamond, Harvard University Press, Cambridge, Massachusetts, pp. 460-490.

Connor, M.S., J.M. Teal and I. Valiela, 1982. The effect of feeding by mud snails, Ilyanassa obsoleta (Say), on the structure and metabolism of a laboratory benthic algal community. J. Exp. Mar. Biol. Ecol. 65:29-45.

Crane, J., 1957. Basic patterns of display in fiddler crabs (Ocypodidae, genus Uca). Zoologica 42:69-82.

Crane, J., 1958. Aspects of social behavior in fiddler crabs, with special reference to Uca maracoani (Latreille). Zoologica 43:113-130.

References

Crane, J., 1975. *Fiddler Crabs of the World. Ocypodidae: Genus Uca*. Princeton University Press, New Jersey, 736 pp.

Crichton, O.W., 1960. Marsh crab: intertidal tunnel-maker and grass-eater. Estuar. Bull. **5**:3-10.

Dayton, P.K., 1984. Processes structuring some marine communities: are they general? In, *Ecological Communities: Conceptual Issues and the Evidence*, edited by D.R. Strong, Jr., D. Simberloff, L.G. Abele and A.B. Thistle, Princeton University Press, New Jersey, pp. 181-197.

DeCoursey, P.J. (editor), 1976. *Biological Rhythms in the Marine Environment*. University of South Carolina Press, Columbia, 283 pp.

DeCoursey, P.J., 1979. Egg-hatching rhythms in three species of fiddler crabs. In, *Cyclic Phenomena in Marine Plants and Animals*, edited by E. Naylor and R.G. Hartnoll, Pergamon Press, Oxford, pp. 399-406.

DeCoursey, P.J., 1983. Biological timing. In, *The Biology of the Crustacea, Vol. 7: Behavior and Ecology*, edited by F.J. Vernberg and W.B. Vernberg, Academic Press, New York, pp. 107-162.

Dieleman, J., 1979. Swimming Rhythms, migration and breeding cycles in the estuarine amphipods *Gammarus chevreuxi* and *Gammarus zaddachi*. In, *Cyclic Phenomena in Marine Plants and Animals*, edited by E. Naylor and R.G. Hartnoll, Pergamon Press, Oxford, pp. 415-422.

Dye, A.H., 1978. Diurnal vertical migrations of meiofauna in an estuarine sand flat. Zool. Afr. **13**:201-205.

Dye, A.H. and T.A. Lasiak, 1986. Microbenthos, meiobenthos and fiddler crabs: trophic interactions in a tropical mangrove sediment. Mar. Ecol. Progr. Ser. **32**:259-264.

Efford, I.E., 1965. Aggregation of the sand crab, *Emerita analoga*. J. Anim. Ecol. **34**:63-75.

Ekdale, A.A., R.G. Bromley and S.G. Pemberton. 1984. *Ichnology: Trace Fossils in Sedimentology and Stratigraphy*. Soc. Economic Paleontol. Minerol., Tulsa, Oklahoma, pp. 79-87.

Enright, J.T., 1961. Pressure sensitivity of an amphipod. Science **133**:758-760.

Enright, J.T., 1963. The tidal rhythm of activity of a sand-beach amphipod. Zeit. Vergl. Physiol. **46**:276-313.

Enright, J.T., 1972. A virtuoso isopod. Circa-lunar rhythms and their tidal fine structure. J. Comp. Physiol. **77**:141-162.

Enright, J.T., 1974. Relationships between circannual rhythms and endogenous lunar and tidal rhythms. In, *Circannual Clocks: Annual Biological Rhythms*, edited by E.T. Pengelley, Academic Press, New York, pp. 249-251.

References

Farrow, G.E., 1971. Back-reef and lagoonal environments of Aldabra Atoll distinguished by their crustacean burrows. Symp. Zool. Soc. Lond. **28**:455-500.

Fenwick, G.D., 1984. Partitioning of a rippled sand habitat by five infaunal crustaceans. J. Exp. Mar. Biol. Ecol. **83**:53-72.

Fielder, D.R., 1970. The feeding behaviour of the sand crab *Scopimera inflata* (Decapoda, Ocypodidae). J. Zool. Lond. **160**:35-49.

Fielder, D.R. and M.B. Jones, 1978. Observations of feeding behaviour in two New Zealand mud crabs (*Helice crassa* and *Macrophthalmus hirtipes*). Mauri Ora **6**:41-46.

Fish, J.D. and S. Fish, 1972. The swimming rhythm of *Eurydice pulchra* and a possible explanation of intertidal migration. J. Exp. Mar. Biol. Ecol. **8**:195-200.

Frith, D.W., R. Tantanasiriwong and O. Bhatia, 1976. Zonation and abundance of macrofauna on a mangrove shore, Phuket Island. Res. Bull. Phuket Mar. Biol. Ctr. **10**:1-37.

Gallagher, E.D., P.A. Jumars and D.D. Trueblood, 1983. Facilitation of soft-bottom benthic succession by tube builders. Ecology **64**:1200-1216.

Gamble, F.W. and F. Keeble, 1903. The bionomics of *Convoluta roscoffensis*, with special reference to its green cells. Proc. Roy. Soc. Lond. **72**:93-98.

Garrity, S.D., 1984. Some adaptations of gastropods to physical stress on a tropical rocky shore. Ecology **65**:559-574.

Garrity, S.D. and S.C. Levings, 1983. Homing to scars as a defense against predators in the pulmonate limpet *Siphonaria gigas* (Gastropoda). Mar. Biol. **72**:319-324.

Gosselink, J.G. and C.J. Kirby, 1974. Decomposition of salt marsh grass, *Spartina alterniflora* Loisel. Limnol. Oceanogr. **19**:825-832.

Gray, J.S., 1974. Animal-sediment relationships. Oceanogr. Mar. Biol. Ann. Rev. **12**:223-261.

Green, P.A. and D.T. Anderson, 1973. The first zoea larvae of the estuarine crabs *Sesarma erythrodactyla* Hess, *Helograpsus haswellianus* (Whitelegge) and *Chasmagnathus laevis* Dana (Brachyura, Grapsidae, Sesarminae). Proc. Linn. Soc. New South Wales **98**:13-28.

Griffin, D.J.G., 1965. The behaviour of shore crabs. Aust. Nat. Hist., **15**:87-91.

Griffin, D.J.G., 1968. Social and maintenance behaviour in two Australian ocypodid crabs (Crustacea: Brachyura). J. Zool. Lond. **156**:291-305.

References

Griffin, D.J.G., 1971. The ecological distribution of grapsid and ocypodid shore crabs (Crustacea: Brachyura) in Tasmania. J. Anim. Ecol. 40:597-621.

Gum, W.L., 1985. The diet, feeding behaviour and aspects of the general biology of Tetractenos hamiltoni (Gray and Richardson) at Careel Bay, Sydeny, New South Wales. Unpublished B.Sc. (Honours) Thesis, University of Sydney, New South Wales, 68 pp.

Hamilton, P.V., 1976. Predation on Littorina irrorata (Mollusca: Gastropoda) by Callinectes sapidus (Crustacea: Portunidae). Bull. Mar. Sci. 26:403-409.

Hartnoll, R.G., 1965. Notes on the marine grapsid crabs of Jamaica. Proc. Linn. Soc. Lond. 176:113-147.

Hartnoll, R.G., 1969. Mating in the Brachyura. Crustaceana 16:161-181.

Hartnoll, R.G., 1973. Factors affecting the distribution and behaviour of the crab Dotilla fenestrata on east African shores. Estuar. Coast. Mar. Sci. 1:137-152.

Henmi, Y., 1984. The description of wandering behavior and its occurrence varying in different tidal areas in Macrophthalmus japonicus (De Haan) (Crustacea: Ocypodidae). J. Exp. Mar. Biol. Ecol. 84:211-224.

Herrnkind, W.F., 1968. Adaptive visually-directed orientation in Uca pugilator. Am. Zool. 8:585-598.

Hoffman, J.A., J. Katz and M.D. Bertness, 1984. Fiddler crab deposit-feeding and meiofaunal abundance in salt marsh habitats. J. Exp. Mar. Biol. Ecol. 82:161-174.

Hogue, E.W. and C.B. Miller, 1981. Effects of sediment microtopography on small-scale spatial distributions of meiobenthic nematodes. J. Exp. Mar. Biol. Ecol. 53:181-191.

Hutchings, P.A. and H.F. Recher, 1974. The fauna of Careel Bay with comments on the ecology of mangrove and sea-grass communities. Aust. Zool. 18:99-128.

Hutchings, P.A. and H.F. Recher, 1982. The fauna of Australian mangroves. Proc. Linn. Soc. New South Wales 106:83-121.

Hutchings, P.A., J. Pickard, H.F. Recher and P.B. Wheate, 1977. A survey of mangroves at Brooklyn, Hawkesbury River, New South Wales. Operculum (Jan.):105-112.

Hyatt, G.W., 1977. Field studies of size-dependent changes in waving display and other behavior in the fiddler crab, Uca pugilator (Brachyura, Ocypodidae). Mar. Behav. Physiol. 4:283-292.

Hyatt, G.W. and M. Salmon, 1978. Combat in the fiddler crabs Uca pugilator and U. pugnax: a quantitative analysis. Behaviour 65:182-211.

References

Hylleberg, J., 1975. Selective feeding by Abarenicola pacifica with notes on Abarenicola vagabunda and a concept of gardening in lugworms. Ophelia 14:113-137.

Jones, D.A., 1984. Crabs of the mangal ecosystem. In, Hydrobiology of the Mangal, edited by F.D. Por and I. Dor, W. Junk, The Hague, pp. 89-109.

Jones, D.A. and C. st C. Hobbins, 1985. The role of biological rhythms in some sand beach cirolanid isopoda. J. Exp. Mar. Biol. Ecol. 93:47-59.

Jones, M.B. and M.J. Simons, 1982. Habitat preferences of two estuarine burrowing crabs Helice crassa Dana (Grapsidae) and Macrophthalmus hirtipes (Jacquinot)(Ocypodidae). J. Exp. Mar. Biol. Ecol. 56:49-62.

Kohn, A.J., 1983. Microhabitat factors affecting abundance and diversity of Conus on coral reefs. Oecologia 60:293-301.

Levings, S.C. and S.D. Garrity, 1983. Diel and tidal movement of two co-occurring neritid snails: differences in grazing patterns on a tropical rocky shore. J. Exp. Mar. Biol. Ecol. 67:261-278.

Levings, S.C. and S.D. Garrity, 1984. Grazing patterns in Siphonaria gigas (Molllusca, Pulmonata) on the rocky Pacific coast of Panama. Oecologia 64:152-159.

Lighter, F., 1974. A note on the behavioral spacing mechanism of the ghost crab Ocypode ceratophthalmus (Pallus)(Decapoda, Family Ocypodidae). Crustaceana 27:312-314.

Lipcius, R.N. and W.F. Herrnkind, 1982. Molt cycle alterations in behavior, feeding and diel rhythms of a decapod crustacean, the spiny lobster Panulirus argus. Mar. Biol. 68:241-252.

Macnae, W., 1967. Zonation within mangroves associated with estuaries in North Queensland. In, Estuaries, edited by G.H. Lauff, Amer. Assoc. Adv. Sci., Washington, pp. 432-441.

Macnae, W., 1968. A general account of the fauna and flora of mangrove swamps and forests in the Indo-West Pacific Region. Adv. Mar. Biol. 6:73-270.

Macnae, W. and M. Kalk, 1962. The fauna and flora of sand flats at Inhaca Island, Mocambique. J. Anim. Ecol. 31:93-128.

McCormick, W.A., 1978. The ecology of benthic macrofauna in New South Wales mangrove swamps. Unpublished M.Sc. Thesis, University of New South Wales, Kensington, 333 pp.

McGuinness, K.A. and A.J. Underwood, 1987. Habitat structure and the nature of communities on intertidal boulders. J. Exp. Mar. Biol. Ecol. (in press).

McKillup, S.C. and A.J. Butler, 1979. Cessation of hole-digging by the crab Helograpsus haswellianus: a resource-conserving adaptation. Mar. Biol. 50:157-161.

References

McLachlan, A., T. Erasmus and J.P. Furstenberg, 1977. Migrations of sandy beach meiofauna. Zool. Afr. 12:254-277.

Menge, B.A. and J. Lubchenco, 1981. Community organization in temperate and tropical rocky intertidal habitats: prey refuges in relation to consumer pressure gradients. Ecol. Monogr. 51:429-450.

Miller, D.C., 1961. The feeding mechanism of fiddler crabs with ecological considerations of feeding adaptations. Zoologica 46:89-100.

Montague, C.L., 1980. A natural history of temperate western Atlantic fiddler crabs (genus Uca) with reference to their impact on the salt marsh. Contrib. Mar. Sci. 23:25-55.

Montague, C.L., 1982. The influence of fiddler crab burrows and burrowing on metabolic processes in salt marsh sediments. In, Estuarine Comparisons, edited by V.S. Kennedy, Academic Press, New York, pp. 283-301.

Moran, M.J., 1985. The timing and significance of sheltering and foraging behaviour of the intertidal gastropod Morula marginalba Blainville (Muricidae). J. Exp. Mar. Biol. Ecol. 93:103-114.

Murai, M., S. Goshima and Y. Nakasone, 1982. Some behavioral characteristics related to food supply and soil texture of burrowing habitats observed on Uca vocans vocans and Uca lactea perplexa. Mar. Biol. 66:191-197.

Musgrave, A., 1929. Life in a mangrove swamp. Aust. Mus. Mag. 3:340-348.

Nakasone, Y., 1982. Ecology of the fiddler crab Uca (Thalassuca) vocans vocans (Linnaeus)(Decapoda: Ocypodidae). I. Daily activity in warm and cold seasons. Res. Popul. Ecol. 24:97-109.

Naylor, E., 1958. Tidal and diurnal rhythms of locomotor activity in Carcinus maenas (L.). J. Exp. Biol. 35:602-610.

Naylor, E. and R.G. Hartnoll (editors), 1979. Cyclic Phenomena in Marine Plants and Animals. Pergamon Press, Oxford, 477 pp.

Naylor, E., R.J.A. Atkinson and B.G. Williams, 1971. External factors influencing the tidal rhythm of shore crabs. J. Interdiscipl. Cycle Res. 2:173-180.

Oliver, J.S. and P.N. Slattery, 1985. Destruction and opportunity on the seafloor: effects of gray whale feeding. Ecology 66:1965-1975.

Ono, Y., 1959. The ecological studies on brachyura in the estuary. Bull. Mar. Biol. Sta. Asamushi 9:145-148.

Ono, Y., 1962. On the habitat preference of ocypoid crabs. Mem. Fac. Sci. Kyushu University, Ser. E (Biol.) 3:143-163.

Pace, M.L., S. Shimmel and W.M. Darley, 1979. The effect of grazing by a gastropod, Nassarius obsoletus, on the benthic microbial community of a salt marsh mudflat. Estuar. Coast. Mar. Sci. 9:121-134.

References

Palmer, J.D., 1967. Daily and tidal components in the persistent rhythmic activity of the crab Sesarma. Nature (London) 215:64-66.

Palmer, J.D., 1974. Biological Clocks in Marine Organisms. J. Wiley and Sons, New York, 173 pp.

Palmer, J.D. and F.E. Round, 1967. Persistent, vertical-migration rhythms in benthic microflora. VI. The tidal and diurnal nature of the rhythm in the diatom Hantzschia virgata. Biol. Bull. 132:44-55.

Peterson, C.H., 1979. Predation, competitive exclusion, and diversity in the soft-sediment benthic communities of estuaries and lagoons. In, Ecological Processes in Coastal and Marine Systems, edited by R.J. Livingston, Plenum Publishing Corp., pp. 233-264.

Powers, L.W., 1975. Fiddler crabs in a non-tidal environment. Contrib. Mar. Sci. 19:67-78.

Powers, L.W. and J.F. Cole, 1976. Temperature variation in fiddler crab microhabitats. J. Exp. Mar. Biol. Ecol. 21:141-157.

Reise, K., 1985. Tidal Flat Ecology: An Experimental Approach to Species Interactions. Springer-Verlag, Berlin, 191 pp.

Rhoads, D.C., 1967. Biogenic reworking of intertidal and subtidal sediments in Barnstable Harbor and Buzzards Bay, Massachusetts. J. Geol. 75:461-476.

Rhoads, D.C., 1974. Organism-sediment relations on the muddy sea floor. Oceanogr. Mar. Biol. Ann. Rev. 12:263-300.

Rhoads, D.C. and D.K. Young, 1970. The influence of deposit-feeding organisms on sediment stability and community trophic structure. J. Mar. Res. 28:150-178.

Rhoads, D.C. and D.K. Young, 1971. Animal-sediment relations in Cape Cod Bay, Massachusetts. II. Reworking by Molpadia oolitica (Holothuroidea). Mar. Biol. 11:255-261.

Ringold, P., 1979. Burrowing, root mat density, and the distribution of fiddler crabs in the eastern United States. J. Exp. Mar. Biol. Ecol. 36:11-21.

Robertson, J.R., K. Bancroft, G. Vermeer and K. Plaisier, 1980. Experimental studies on the foraging behavior of the sand fiddler crab Uca pugilator (Bosc 1802). J. Exp. Mar. Biol. Ecol. 44:67-83.

Salmon, M., 1983. Acoustic 'calling' by fiddler and ghost crabs. In, Papers from the Conference on the Biology and Evolution of Crustacea, Australian Museum, Memoir 18, pp. 63-76.

Salmon, M., 1984. The courtship aggression and mating system of a "primitive" fiddler crab (Uca vocans: Ocypodidae). Trans. Zool. Soc. Lond. 37:1-50.

Redfield, J.A., 1982. Trophic relationships in mangrove communities. In, Mangrove Ecosystems in Australia: Structure, Function and Management, edited by B.F. Clough, Australian National University Press, Canberra, pp. 259-262.

References

Salmon, M. and G.W. Hyatt, 1983. Spatial and temporal aspects of reproduction in North Carolina fiddler crabs (*Uca pugilator* Bosc). J. Exp. Mar. Biol. Ecol. *70*:21-43.

Salmon, M., W.H. Seiple and S.G. Morgan, 1986. Hatching rhythms of fiddler crabs and associated species at Beaufort, North Carolina. J. Crustac. Biol. *6*:24-36.

Sasekumar, A., 1974. Distribution of macrofauna on a Malayan mangrove shore. J. Anim. Ecol. *43*:51-70.

Saunders, D.S., 1977. *An Introduction to Biological Rhythms*. Blackie and Son, Ltd., London, 170 pp.

Seiple, W. and M. Salmon, 1982. Comparative social behavior of two grapsid crabs, *Sesarma reticulatum* (Say) and *S. cinereum* (Bosc). J. Exp. Mar. Biol. Ecol. *62*:1-24.

Shinn, E.A., 1968. Burrowing in recent lime sediments of Florida and the Bahamas. J. Paleont. *42*:879-894.

Smith, W.K. and P.C. Miller, 1973. The thermal ecology of two south Florida fiddler crabs, *Uca rapax* Smith and *Uca pugilator* Bosc. Physiol. Zool. *46*:186-207.

Snedecor, G.W. and W.G. Cochran, 1980. *Statistical Methods* (Seventh Edition). Iowa State University Press, Ames, 507 pp.

Snelling, B., 1959. The distribution of intertidal crabs in the Brisbane River. Aust. J. Mar. Freshw. Res. *10*:67-83.

Sousa, W.P., 1985. Disturbance and patch dynamics on rocky intertidal shores. In, *Natural Disturbance: The Patch Dynamics Perspective*, edited by S.T.A. Pickett and P.S. White, Academic Press, New York, pp. 101-124.

Teal, J.M., 1958. Distribution of fiddler crabs in Georgia salt marshes. Ecology *39*:185-193.

Thistle, D., 1980. The response of a harpacticoid copepod community to a small-scale natural disturbance. J. Mar. Res. *38*:381-395.

Underwood, A.J., 1979. The ecology of intertidal gastropods. Adv. Mar. Biol. *16*:111-210.

Underwood, A.J., 1981. Techniques of analysis of variance in experimental marine biology and ecology. Oceanogr. Mar. Biol. Ann. Rev. *19*:513-605.

Underwood, A.J. and E.J. Denley, 1984. Paradigms, explanations, and generalizations in models for the structure of intertidal communities on rocky shores. In, *Ecological Communities: Conceptual Issues and the Evidence*, edited by D. Strong, Jr., D. Simberloff, L.G. Abele and A.B. Thistle, Princeton University Press, New Jersey, pp. 151-180.

References

Valiela, I., D.F. Babiec, W. Atherton, S. Seitzinger and C. Krebs, 1974. Some consequences of sexual dimorphisms: feeding in male and female fiddler crabs, Uca pugnax (Smith). Biol. Bull. 147:652-660.

VanBlaricom, G.R., 1982. Experimental analyses of structural regulation in a marine sand community exposed to oceanic swell. Ecol. Monogr. 52:283-305.

Wada, K., 1985. Unique foraging behavior of Dotillopsis brevitarsis (Crustacea, Brachyura: Ocypodidae). J. Ethol. 3:76-78.

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.

Ward, M., 1928. The habits of our common shore crabs. Aust. Mus. Mag. 2:242-247.

Warner, G.F., 1967. The life history of the mangrove tree crab, Aratus pisoni. J. Zool. Lond. 153:321-335.

Warner, G.F., 1969. The occurrence and distribution of crabs in a Jamaican mangrove swamp. J. Anim. Ecol. 38:379-389.

Warner, G.F., 1977. The Biology of Crabs. Van Nostrand Reinhold Co., New York, 202 pp.

Warren, J.H., 1985. Climbing as an avoidance behaviour in the salt marsh periwinkle, Littorina irrorata (Say). J. Exp. Mar. Biol. Ecol. 89:11-28.

Wells, R.A., 1980. Activity pattern as a mechanism of predator avoidance in two species of acmaeid limpet. J. Exp. Mar. Biol. Ecol. 48:151-168.

Whiting, N.H. and G.A. Moshiri, 1974. Certain organism-substrate relationships affecting the distribution of Uca minax (Crustacea: Decapoda). Hydrobiologia 44:481-493.

Wilkens, J.L. and M. Fingerman, 1965. Heat tolerance and temperature relationships of the fiddler crab, Uca pugilator, with reference to body coloration. Biol. Bull. 128:133-141.

Williams, B.G., 1969. The rhythmic activity of Hemigrapsus edwardsi (Hilgendorf). J. Exp. Mar. Biol. Ecol. 3:215-223.

Williams, B.G., E. Naylor and T.D. Chatterton, 1985. The activity patterns of New Zealand mud crabs under field and laboratory conditions. J. Exp. Mar. Biol. Ecol. 89:269-282.

Williams, J.A., 1979. A semi-lunar rhythm of locomotor activity and moult synchrony in the sand-beach amphipod Talitrus saltator. In, Cyclic Phenomena in Marine Plants and Animals, edited by E. Naylor and R.G. Hartnoll, Pergamon Press, Oxford, pp. 407-414.

References

Wilson, W.H., 1979. Community structure and species diversity of the sedimentary reefs constructed by *Petaloproctus socialis* (Polychaeta: Maldanidae). J. Mar. Res. *37*:623-641.

Winer, B.J., 1971. *Statistical Principles in Experimental Design* (Second Edition). International Student Edition, McGraw-Hill Kogakusha Ltd., Tokyo, 907 pp.

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*:161-184.

Woodin, S.A., 1983. Biotic interactions in recent marine sedimentary environments. In, *Biotic Interactions in Recent and Fossil Benthic Communities*, edited by M.J.S. Tevesz and P.L. McCall, Plenum Press, New York, pp. 3-38.

Woodin, S.A., 1985. Effects of defecation by arenicolid polychaete adults on spionid polychaete juveniles in field experiments: selective settlement or differential mortality. J. Exp. Mar. Biol. Ecol. *87*:119-132.

Yates, R.W., 1978. Aspects of the ecology and reproductive biology of crabs in a mangrove swamp at Patonga, New South Wales. Unpublished M.Sc. Thesis, University of Sydney, New South Wales, 135 pp.

Zann, L.P., 1973. Relationships between intertidal zonation and circatidal rhythmicity in littoral gastropods. Mar. Biol. *18*:243-250.

Zucker, N., 1974. Shelter building as a means of reducing territory size in the fiddler crab, *Uca terpsichores* (Crustacea: Ocypodidae). Am. Midl. Nat. *91*:225-236.

Zucker, N., 1976. Behavioral rhythms in the fiddler crab *Uca terpsichores*. In, *Biological Rhythms in the Marine Environment*, edited by P.J. DeCoursey, University of South Carolina Press, Columbia, pp. 145-159.

Zucker, N., 1983. Courtship variation in the neo-tropical fiddler crab *Uca deichmanni*: another example of female incitation to male competition? Mar. Behav. Physiol. *10*:57-79.

Zwarts, L., 1985. The winter exploitation of fiddler crabs *Uca tangeri* by waders in Guinea-Bissau. Ardea *73*:3-12.