ASPECTS OF THE ECOLOGY AND REPRODUCTIVE BIOLOGY OF CRABS IN A MANGROVE SWAMP AT PATONGA, N.S.W.

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Declaration

I certify that the work described in this study is the result of my own research conducted during the period from February, 1974, to January, 1978.

R. W. Yates.

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SUMMARY

Populations of crabs in a mangrove swamp at Patonga, N.S.W., were sampled from September, 1974, to February, 1976, to determine seasonal patterns of distribution and abundance in relation to height on the shore.

The mangrove swamp was divided into four zones on the basis of the relative numbers of the two species of mangrove present, Avicennia marina and Aegiceras corniculatum. The relative numbers of oysters, and saplings and pneumatophores of mangroves, in each zone were determined.

A number of methods of sampling crabs were compared. Baited pitfall traps proved most suitable to sample grapsids and xanthids. Photographic censuses were used in conjunction with the data from traps to estimate relative abundance of ocypodids.

The distributions of the crabs showed zonation which corresponded to the zonation of the mangrove trees. Two ocypodids, Heloecius cordiformis and Australoplax tridentata, were found in greatest numbers in the lowest zone on the shore and their numbers decreased at higher levels. Pilumnopeus serratifrons and Ilyograpsus paludicola were found only in the lowest zone. Sesarma erythrodactyla were found in greatest numbers in the highest zone and their numbers decreased at lower levels on the shore. Helograpsus haswellianus were found only in the highest zone. Paragrapsus laevis were found in greatest numbers in the second lowest zone. Small numbers of Helice leachii

were found on the higher levels on the shore.

There were seasonal changes in the relative abundance of the crabs. These were closely related to seasonal changes in activity of the crabs. All species were most abundant in the warmer months of the year, except P. laevis, which were most abundant in winter.

Changes in the relative abundance of crabs from zone to zone were compared with the reproductive cycles of the crabs. Reproductive cycles were analysed by examination of breeding condition of females, and from analysis of histological sections of gonads. S. erythrodactyla and P. laevis had definite breeding periods; their reproductive cycles reached peaks in Summer and Winter, respectively. H. cordiformis bred throughout the year, but their reproductive cycle reached a peak in winter. It is postulated that gravid S. erythrodactyla and P. laevis migrate to zones lower on the shore to spawn.

The peaks of the breeding seasons and the periods of greatest activity of S. erythrodactyla and P. laevis co-incided; those of H. cordiformis were at different times of the year.

Some of the factors influencing the distribution and abundance and the patterns of zonation of the crabs were examined in the field and in laboratory experiments. Salinity, the amount of organic matter in the soil and the composition of particle sizes of the soil were found to be unimportant. Moisture content of the soil appeared to be important in influencing the distribution of H. cordiformis, P. laevis and A. tridentata. Depth to the water table and period of exposure to air appeared to be

important in the distribution of these three species only because of their effect on the moisture content of the soil. The factors influencing the distribution of S. erythrodactyla were less clear.

The zonation and pattern of relative abundance of these crabs are similar in some respects to the patterns found in other geographical areas. These are discussed with respect to the characteristics of the mangrove swamp at Patonga and the lines of investigation in the present work.

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SECTION I : GENERAL INTRODUCTION

Mangroves dominate an estimated 75% of the world's coastlines between the latitudes 25°N and 25°S (Golley et al., 1962). Their importance in estuarine ecosystems has more recently become apparent: they are more fertile than most marine and terrestrial communities (Golley et al., 1962); the large quantities of organic matter they produce form the base of estuarine food chains; they act as nurseries for many organisms; they harbour a unique fauna (Warner, 1969; Sasekumar, 1974; Frith et al., 1976). Despite this, mangrove swamps throughout the world are being destroyed due to exploitation by man. Between 1966 and 1976 at least 10-15% of mangroves in Thailand were destroyed (Frith et al., 1976). The timber was used for charcoal, building or firewood; areas were cleared for housing, road construction, tin mining, coastal prawn and fish farms. Similar examples can be found around the world (e.g. Berry, 1963; Macnae, 1968). It is important that the ecology of mangroves is studied to assess their value and potential to man before they are completely destroyed.

Most of the ecological literature about mangroves concerns the flora. The species composition of mangrove swamps, the distribution of mangroves along coastlines, the vertical zonation of mangroves on shores and the factors related to these, have been described in many places (e.g. Watson, 1928; Davis, 1940; Dansereau, 1947; Macnae, 1963, 1966, 1967, 1968; Macnae and Kalk, 1962; Clark and Hannon, 1967, 1969; Jones, 1971). The patterns of distribution of the rich fauna and the underlying factors determining these patterns, however, are largely unknown.

Most recent workers (e.g. Warner, 1969; Day, 1974; Sasekumar, 1974; Frith, 1976) have recognised that mangroves harbour a unique fauna, which is not just a "fortuitous association" with mangrove trees as had been suggested earlier (Macnae and Kalk, 1962; Macnae, 1968). This mangrove fauna is adapted to life in the environment produced by the growth of mangrove trees. As Warner (1969) stated: "there is a definite characteristic fauna, depending, not just on the conditions on which the trees depend, but on the environment produced by the presence of the trees." Factors which are characteristic of mangrove swamps and which are created to a great extent by the presence of the mangroves are: the accumulation of mud by the roots of the trees; deposition of organic detritus, including remains of dead animals and plants (mainly leaves of mangroves); shade and reduced air flow (provided by the mangroves) which reduce evaporation and keeps the swamp floor relatively cool and moist. The distributions of the species of animals are not always confined to mangrove swamps, but usually they occur there in greatest numbers.

Species diversity is high within mangrove swamps compared to other intertidal habitats. Frey et al., (1975) found that of 55 species of crustaceans present on the shore at Ao Nam-Bor, Thailand, 37 occurred exclusively within the mangrove forest and only 10 exclusively within the adjacent mud flat and sand flat. The remaining 8 species were found in more than one of these habitats. The groups of macrofauna represented by the most species in mangrove swamps are Polychaeta, Gastropoda and Crustacea.

TABLE 1-1

List of the species of crabs present in the study area in the mangroves at Patonga.

Family Ocypodidae

Heloecius cordiformis (H. Milne Edwards)

Australoplax tridentata (A. Milne Edwards)

Family Grapsidae

Sesarma erythrodactyla (Hess)

Paragrapsus laevis (Dana)

Helograpsus haswellianus (Whitelegge)

Helice leachii (Hess)

Ilyograpsus paludicola (Rathbun) See note on page 3.

Family Xanthidae

Pilumnopeus serratifrons (Kinahan)

One of the most abundant and diverse groups of Crustacea present in mangrove swamps is the Brachyura. The purpose of this study is to describe the vertical distribution and relative abundance on the shore of crabs in a mangrove swamp at Patonga, N.S.W., and to make an attempt to determine the factors controlling these.

A list of the species of crabs encountered during this study, with the taxonomic authorities for the nomenclature used, is shown in Table 1-1. Four of the most abundant species are shown in Figs. 1-1, 1-2, 1-3, 1-4. Positive identification of one small species was not possible. It appeared identical to a species described by Rathbun (1910) and named Camptandrium paludicola. The type locality of this species was reported to be mangrove swamp. This species was subsequently included in the genus Ilyograpsus by Crosnier (1965). The species caught in the present study was tentatively named Ilyograpsus paludicola. Specimens have been lodged with The Australian Museum, Sydney.

Direct comparisons of mangrove shores around the world are difficult. The structure and complexity of mangrove swamps vary greatly. There is variation in the species and the abundance of both mangroves and their fauna, as well as the nature of the substrata in which the mangroves grow. Many mangrove swamps contain channels, mud-banks and lagoons which complicate comparison of the distribution of flora and fauna there with other places. The sampling of crabs is difficult in mangrove swamps. Various sampling techniques have been used by different workers (these are discussed Section 3.21) and data are, therefore, difficult to compare.

As a result, most studies of mangrove macrofauna have been

FIG. 1-1

Sesarma erythrodactyla. A, male (larger crab) and female (x 1/2). B, male (x 2).

A

B

FIG. 1-2

Paragrapsus laevis (x 2) A, male. B, gravid female.

A

B

FIG. 1-3

Heloecius cordiformis (x 1/2) Male and female (below) near burrow.

FIG. 1-4

Australoplax tridentata (male).


CM

qualitative (Verwey, 1930; Dansereau, 1947; Fourmannoir, 1953, 1955; Rodriguez, 1959, 1963; Macnae and Kalk, 1962; Macnae, 1963, 1966, 1967, 1968; Berry, 1963, 1972). More recent studies in which quantitative data are given involved sampling of total macrofauna, and crabs were inadequately sampled (Sasekumar, 1974; Day, 1974; Hutchings and Recher, 1974; Frith et al., 1976). The only study which is confined to the quantitative investigation of crabs in a mangrove swamp is that of Warner (1969). Warner, however, could not successfully sample many of these species of crabs which dig burrows deep into the substratum. Little quantitative data is, therefore, available on the distribution of crabs in mangrove swamps. Despite these difficulties, comparison of studies is useful and reveals similarities among mangrove shores. There are also similarities between the distributions of crabs in mangrove swamps and their distribution on other kinds of intertidal shores.

The vertical distribution of crabs on a mangrove shore in Java was described by Verwey (1930). Verwey described five zones in relation to the crabs present. These were a grapsid zone highest on the shore, followed in order by two Uca zones, a Metaplax zone, and a Scylla zone. Grapsids were found to be more abundant on higher levels on the shore; ocypodids were numerous on lower levels on the shore.

Snelling (1959) recognised four vertical zones on the shores of the Brisbane River. The shore varied from soft mud, dry stony mud to mangrove swamp. The zones were defined in relation to the crabs present. Seven of the species of crabs in the present study were found by Snelling (1959). A Sesarmine

zone was highest on the shore, followed in order by an Ocypodine zone, an Upper and Lower Macrophthalmine zone, the latter reaching down to low water spring tide level (L.W.S.). Snelling compared these zones with those described by Verwey (1930) and found that they were very similar. The only crabs present in the Sesarmine zone were Sesarma erythrodactyla and Helograpsus haswellianus (= Helice haswellianus; Campbell and Griffin, 1966). They were co-dominant (as defined by Endean, Kenny and Stephenson, 1956) in areas above high water neap tide level (H.W.N.) where the mud was hard and stony. In very stony areas H. haswellianus was dominant and S. erythrodactyla subdominant. In one area a mudflat stretched for about 25 m above high water spring tide level (H.W.S.) upshore from a stretch of mangroves. H. haswellianus was the most abundant crab in the mud flat, and it alone was present where the mud was dry and without puddles. In the mangroves below, stretching from H.W.S. to H.W.N. S. erythrodactyla occupied the highest stations.

The Ocypodine zone was occupied by Heloecius cordiformis and a fiddler crab, Uca longidigitum. H. cordiformis was dominant where the ground was gravelly and firm; H. cordiformis and U. longidigitum were co-dominant where mangroves were present; and U. longidigitum was dominant where mangroves were absent or small and sparse.

Australoplax tridentata (= Euplax tridentata; Barnes, 1966) was the dominant crab in the lower reaches of the Upper Macrophthalmine zone, where it burrowed into the soft fine mud or lived under stones. A species tentatively called Cyrtograpsus paludicola by Snelling, and which might be Ilyograpsus paludicola

(see comments by Snelling, 1959), was found in small numbers living under stones in the soft mud of the Upper Macrophthalmine zone. Small numbers of Paragrapsus laevis (mis-identified by Snelling as Paragrapsus gaimardii; Campbell and Griffin, 1966) were also found in the Upper Macrophthalmine zone.

The xanthid Pilumnopeus serratifrons was found under stones at low tide level during the latter stages of a drought. It normally inhabits the shores of Moreton Bay, into which the Brisbane River flows.

Macnae (1966) concluded that most mangrove fauna along the east coast of Australia did not show marked zonation, but rather preference for particular types of habitat. The various species of Sesarma found (including S. erythrodactyla) ranged from high water level down to the seaward fringe. The smaller species were always in the shade of trees, as long as the substratum was firm enough for burrows. H. cordiformis was more often found along the fringes of mangrove swamps or along the banks of creeks. Helice leachii was restricted in its distribution to the upper levels of the shore; Helograpsus haswellianus (= Helice haswellianus; Campbell and Griffin, 1966) was widespread in its distribution.

Warner (1969) studied the distribution of crabs on a mangrove swamp in Jamaica. Warner recognised three zones in relation to crabs:

(i) the Lower Swamp, the characteristic species of which decreased in numbers towards the landward fringe;

(ii) the Upper Swamp, the characteristic species of which decreased in numbers towards the lagoon;

(iii) the Transitional, or Mid-Swamp zone, which contained no characteristic species.

The crabs present included 5 species of grapsids, 2 species of ocypodids and 2 species of xanthids. None of the species occur at Patonga. When Warner included a Supra-littoral zone and a Sub-littoral zone and noted the species present in these zones he found great similarity between the zones he described and those on mangrove shores in Inhaca Island, Mozambique (Macnae and Kalk, 1962), Brazil (Dansereau, 1947) and Java (Verwey, 1930).

Zonation of total macrofauna on mangrove shores has been described in Malaysia (Berry, 1963, 1972; Sasekumar, 1974) and in Thailand (Frith et al., 1976). Of 34 species of crabs found by Sasekumar, 14 were grapsids and 15 ocypodids; of 39 species found by Frith et al., 16 were grapsids and 18 ocypodids. None of the species found in these studies was present at Patonga. In each of these studies species of grapsids were more common on higher levels on the shore; ocypodids on lower levels on the shore.

Three of the species of crabs found in the present study were found on non-mangrove shores in Tasmania by Griffin (1971). They were found on estuarine shores on substrata that consisted predominantly of sand, although sometimes made up of more than 50% clay. Griffin recognised that vertical zones are less clear for crabs than for other major zoning organisms such as barnacles and molluscs. H. haswellianus occupied the highest levels on the shore, ranging from upper midlittoral into the supralittoral fringe; it was most often present where there were large numbers of stones. P. laevis was most often found in the lower mid-

littoral but ranged very widely and extended from the supralittoral fringe down to the infralittoral. It was found in mud banks and Zostera marshes. H. cordiformis was found in open estuaries in the upper midlittoral zone.

From these studies, it can be concluded that the most abundant families of crabs in mangrove swamps are Grapsidae and Ocypodidae. The distribution of crabs within mangrove swamps and on other kinds of shores shows zonation, and while it is not possible to identify zones applicable to mangrove shores in all parts of the world, it is apparent that grapsids are generally more common at higher levels on the shore, and ocypodids are more common lower on the shore.

While the general distribution of crabs in a mangrove swamp can be related to definable zones, individual species within their zones seem to be restricted to particular microhabitats. Ocypodids, such as H. cordiformis, A. tridentata and the various Uca species found on many mangrove shores, spend most of their time in or near their burrows. (Ono, 1959, 1962, 1965; Griffin, 1968, 1971; Macnae, 1968; Warner, 1969; Frith et al., 1976). Grapsids have been found to occupy a wide range of microhabitats within mangrove swamps. They:

(i) inhabit burrows that are probably self-constructed, although Warner (1969) found no evidence that grapsids dug the burrows that they occupied and reported that there was often evidence to the contrary, although he did not describe this evidence;

(ii) inhabit burrows dug by other species of crabs (Macnae, 1963, Hartnoll, 1965; Warner, 1969);

(iii) occupy systems of tunnels or "crab-runs" under the swamp floor, in which several species might live together and which are not constructed by any individual or species in particular (Warner, 1969); and

(iv) live under leaf litter, rocks, timber and other flotsam.

One grapsid, Aratus pisoni, has been observed to climb trees to avoid predation and competition from other species (Hartnoll, 1965; Warner, 1967, 1969). Grapsids were also observed to climb trees by Berry (1963). Xanthids do not construct burrows and are found beneath leaf litter, timber, stones and other flotsam, in burrows apparently constructed by other species of crabs, and in crevices and fissures in mud banks (Snelling, 1959; Warner, 1969; Sasekumar, 1974).

Snelling (1959) commented that the zones that she described (see page 4) might be modified. Species within a zone only occupied those parts of the zone in which a suitable microhabitat existed. H. cordiformis, for example, was only found where the mud was firm enough for its large burrows to be made. On the other hand, some species were found out of their usual zone if a suitable microhabitat existed elsewhere on the shore. A. tridentata (= Euplax tridentata; Barnes, 1966) was often found above H.W.S. in places where the mud was sufficiently wet.

There are no published data on seasonal changes in the vertical distribution of crabs on mangrove shores. The only report of seasonal change in vertical distribution of crabs on a mangrove shore is that of Warner (1967) in Jamaica. Female

Aratus pisoni migrate from higher levels on the shore to the edge of the swamp to hatch their eggs. A similar migration of female crabs has been reported by Ono (1959) from a non-mangrove shore on the River Tatara, in Japan. Female Sesarma haematocheir migrate during the breeding season from high levels on the shore around a stone wall and grassy clay embankment to lower levels on the shore to hatch their eggs.

Daily changes in the vertical distribution of crabs are related to their patterns of behaviour. Ono (1959) reported that several species of grapsids, including S. erythrodactyla, move from the shelter of crevices in a rock wall or from burrows on higher levels on the shores of the River Tatara, down to feeding areas on the mud surface lower on the shore. They return to higher levels on the shore as the tide rises. Griffin (1965, 1968) reported that the movement of H. cordiformis on the surface at low tide is primarily concentrated around the burrow, although H. cordiformis wander away from the entrance of their burrows, often down to the water's edge, to collect mud for the maintenance of their burrows. They return to their burrows as the tide rises. These are, however, only temporary changes in distribution. The extent of daily movements of crabs in mangrove swamps has not been described.

There is little information on changes in the seasonal activity of crabs in mangrove swamps, due to the lack of data on the relative abundance of crabs collected regularly over a year. Seasonal changes in the activity of crabs on mud-flats were observed by Griffin (1968). Heloecius cordiformis and Hemiplax latifrons were present on the surface of the mud at low

tide in large numbers in summer. Courtship display was only found in summer and fighting among crabs was most common then. During winter, however, activity of the crabs was minimal. Crabs sometimes did not emerge from their burrows for several days and then only to feed.

Many authors have commented on the factors that might influence the vertical distribution of the macrofauna in mangrove swamps. Snelling (1959) and Ono (1962, 1965) pointed out that the factors determining vertical distribution on a shore must be considered separately from those limiting distribution along a shore. In many of the published studies total macrofauna was investigated and the relevance of some of the factors considered to the distribution of crabs is unclear.

Two general studies on the factors affecting the vertical distribution of total macrofauna on mangrove shores were conducted by Sasekumar (1974) and Frith et al., (1976). In each of these studies, variations in certain environmental parameters were measured over the study area and correlated with the distribution of fauna. No experiments were conducted to establish any causal relation between any of the environmental variables and the patterns of distribution of the fauna. Neither study reached any firm conclusions about factors affecting the distribution of the crabs. Variations in temperature, salinity and hydrogen-ion concentration were found to be unimportant. Both workers concluded that a number of factors were involved and that these were probably different for different species of crabs. Sasekumar (1974) concluded that tidal exposure, grain size of the substratum, availability of food and "other factors"

probably interacted to determine the distribution of crabs. Frith et al., (1976) listed particle size and the consolidation, organic content and moisture content of the substrata and/or tidal factors as significant factors determining the distribution of crabs. These authors suggested that the particle size of the soil was probably important in the distribution of ocypodids. Sasekumar suggested that Sesarma species were generally absent from soft, silty substrata of streams and river banks. Sasekumar also suggested that Uca species preferred high ground and firm substrata, whilst others preferred silty soil and, probably, to be near water.

Other workers in mangrove environments and on other types of estuarine shores who have investigated the vertical distribution of fauna, have commented on the factors that might influence the distribution of the fauna.

Macnae (1962) and Berry (1963), working in mangrove swamps in Mozambique and Malaysia, respectively, suggested that factors such as tidal oscillation, the nature and consolidation of the substratum, the level of the water table, the availability of shade, resistance to water loss and the availability of organic debris suitable for food might be important factors influencing the vertical distribution of fauna.

Warner (1969) found a correlation between the zonation of crabs and tidal levels, and commented on the role of microhabitats within the swamp which enabled some species to avoid desiccation and predation. Burrows, crab runs and hiding places under flotsam were mentioned.

Snelling (1959) concluded that the water content of the

soil was the principal factor limiting vertical distribution of crabs, rather than period of exposure to air. This explained why Australoplax tridentata (= Euplax tridentata; Barnes, 1966) was often found about H.W.S., but was restricted to situations where the mud was very wet, and why H. cordiformis was only found where the mud was firm enough for its large burrows to be made.

Ono (1959, 1962) sampled ocypodid and grapsid crabs in the estuary of the Tatara River, on mud and sand tidal flats. He concluded that while the duration of exposure time decided the intertidal habitat of the ocypodids and grapsids as a whole, soil texture and some interspecific interaction determined the distribution of individual species of ocypodids.

Griffin (1971) sampled crabs in Tasmania on substrata ranging from exposed rocky shores to sand and mud flats. He listed the nature of the substratum, availability and type of cover, salinity range, exposure to wave action, and length of time of exposure to air as major factors determining the distribution of crabs. Griffin noted that the vertical distribution of crabs is largely dependent on shelter where they are less subject to fluctuations in relative humidity.

Clearly, there are many factors that might determine the vertical distribution of crabs in a mangrove swamp. As yet, the influence of these factors on vertical distribution of crabs is unclear.

A complete understanding of the factors influencing the distribution and activity of crabs is not possible without a knowledge of their reproductive cycles. It has already been noted that some gravid female crabs migrate to lower levels on

the shore to spawn (page 9). The only published information on the reproductive biology of species present at Patonga is a list of months when some of the species are known to be gravid (Griffin, 1971). The reproductive cycles of crabs on other shores have been studied by Broekhuysen (1941), Hiatt (1948), Naylor (1962), Gifford (1962), Knudson (1964), Warner (1967), Griffin (1969), and Kon and Honma (1970).

The specific aims of this study are:-

(i) to describe the distribution and relative abundance in relation to height on the shore of crabs in a mangrove swamp at Patonga, N.S.W.,

(ii) to determine whether vertical distribution changes seasonally over a twelve month period,

(iii) to discover what factors determine the vertical distribution of the crabs, and

(iv) to describe the reproductive condition of the most common species of crabs present over a twelve month period and to see what bearing this has on (ii) above.

SECTION 2. DESCRIPTION OF STUDY AREA

2.1 LOCATION AND CHOICE OF STUDY AREA

The area chosen for the present study was a stand of mangroves near the mouth of Patonga Creek, Patonga, New South Wales. Patonga (33^{o} 33' S; 151^{o} 16' E) is located 60 km north of Sydney on the shore of Broken Bay at the mouth of the Hawkesbury River. At the level of the study area Patonga Creek is tidal and is protected from strong wave action by a spit of land across its mouth, which is connected to Broken Bay by a narrow channel (Figs. 2-1, 2-2).

The site was selected for the study for the reasons set out below.

(i) Only two species of mangrove tree were present: the grey mangrove Avicennia marina (Forst.) Vierh. and the river or black mangrove Aegiceras corniculatum (L.) Blanco. The site thus offered an opportunity to study a mangrove area which was relatively simple. Macnae (1966) and Jones (1971) have shown that the number of mangrove tree species and the complexity of mangrove swamps increases greatly further north into the tropics along the eastern coast of Australia. Twenty-seven species of mangrove tree are reported to be present on the far north coast of Queensland north of the Daintree River (Jones, 1971). Other major studies of mangrove fauna have been confined principally to the very complex mangrove communities of the tropics (e.g. Java (Verwey, 1930), Malaya (Berry, 1963, 1972; Sasekumar, 1974), Thailand (Frith et al.,

FIG. 2-1

Map of Patonga Creek. Transects A and B across the study area are indicated by broken lines. The position of the Temporary Bench Mark at the upper end of Transect A is marked by *.

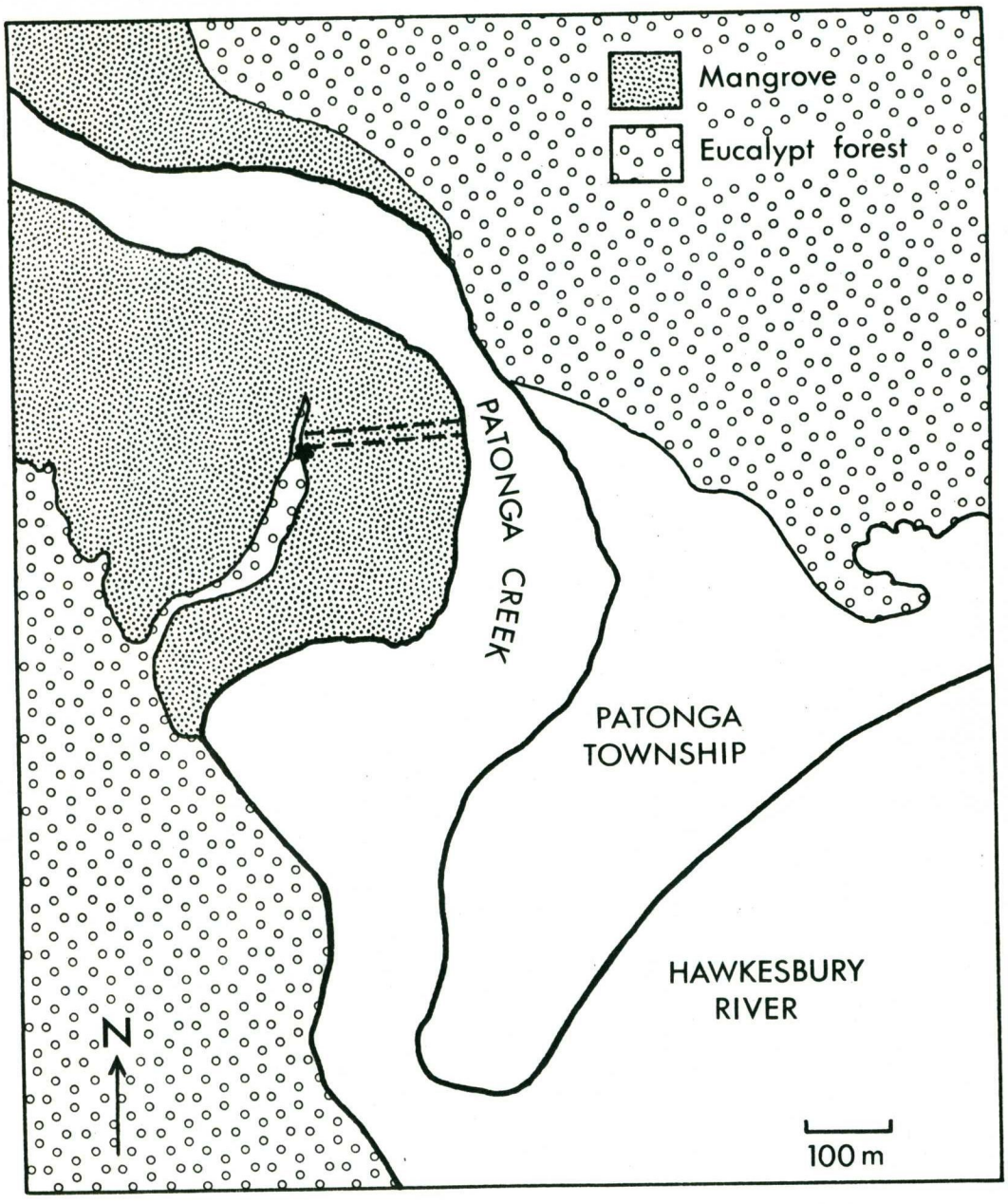
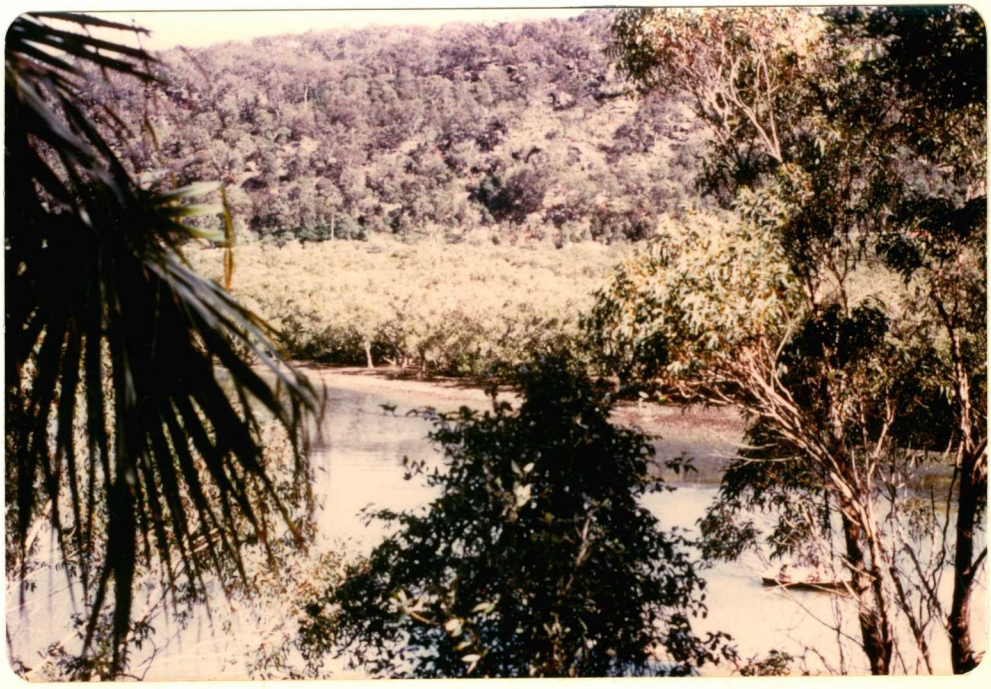

Mangrove
Eucalypt forest
PATONGA CREEK
PATONGA
TOWNSHIP
HAWKESBURY
RIVER
N
100 m

FIG. 2-2

Views of Patonga Creek. A, showing mouth of Patonga Creek, oyster leases and edge of mangrove swamp (in lower right corner). B, showing mangrove study area.

A

B



1976), Brazil (Dansereau, 1947), Venezuela (Rodriguez, 1959, 1963), Mozambique (Macnae and Kalk, 1962)).

(ii) The stand of mangroves was relatively compressed. The maximum distance from the junction of the mangrove swamp with the Zostera weed bed to the back of the swamp at its junction with the landward fringe was 181 m. This greatly facilitated movement of equipment throughout the study.

(iii) The area was free of any serious problems of pollution which might have affected the animal or plant species during the period of the study. This was in marked contrast to mangrove areas in the Sydney region, many of which have been damaged or destroyed by the effects of pollution of the river systems.

(iv) The mangrove stand was located within an oyster lease and was under regular surveillance of local oyster farmers. This ensured minimal human interference to the area itself or to any traps or other equipment which was left in the field.

2.2 SURVEY OF STUDY AREA

2.21 Variation in Vertical Height on the Shore

Initially the study area was surveyed to measure variation in vertical height on the shore from its junction with the Zostera weed bed to its junction with the terrestrial fringe.

Materials and Methods

As no Land Survey Bench Mark was available it was not possible to relate tidal levels on the shore to existing official surveys. Relative heights on the shore for this study were therefore taken from a Temporary Bench Mark (TBM). All heights were related to this, to allow comparisons within and across the study area. The TBM was established at the back of the mangrove swamp at the junction with the terrestrial fringe at the base of a large tree (Casuarina glauca (Sprieng.) Sieb.). It was arbitrarily assigned a vertical height of +10.00 m. The heights of points spaced every 5 m along a transect, A, from the TBM to the junction with the Zostera weed bed were measured relative to the height of the TBM using a surveyor's level. As well, nine mangrove trees along this transect were marked as reference points of the distance to the back of the swamp. The height of a second point at the junction of the mangrove swamp and terrestrial fringe and 53 m north of the TBM was measured relative to the height of the TBM. A second transect, B, was made from this second point to the junction with the Zostera weed bed in a similar fashion to the first. Eight mangrove trees along this transect were marked for use as reference points of the distance from the back of the swamp.

Results

The variation in vertical height along transects A and B is shown in Fig. 2-3.

FIG. 2-3

Variation in vertical height on the shore at the Patonga study site. Vertical heights are measured relative to the height of a temporary bench mark (TBM) arbitrarily assigned a vertical height of 10 m. Arrows indicate junctions between zones.

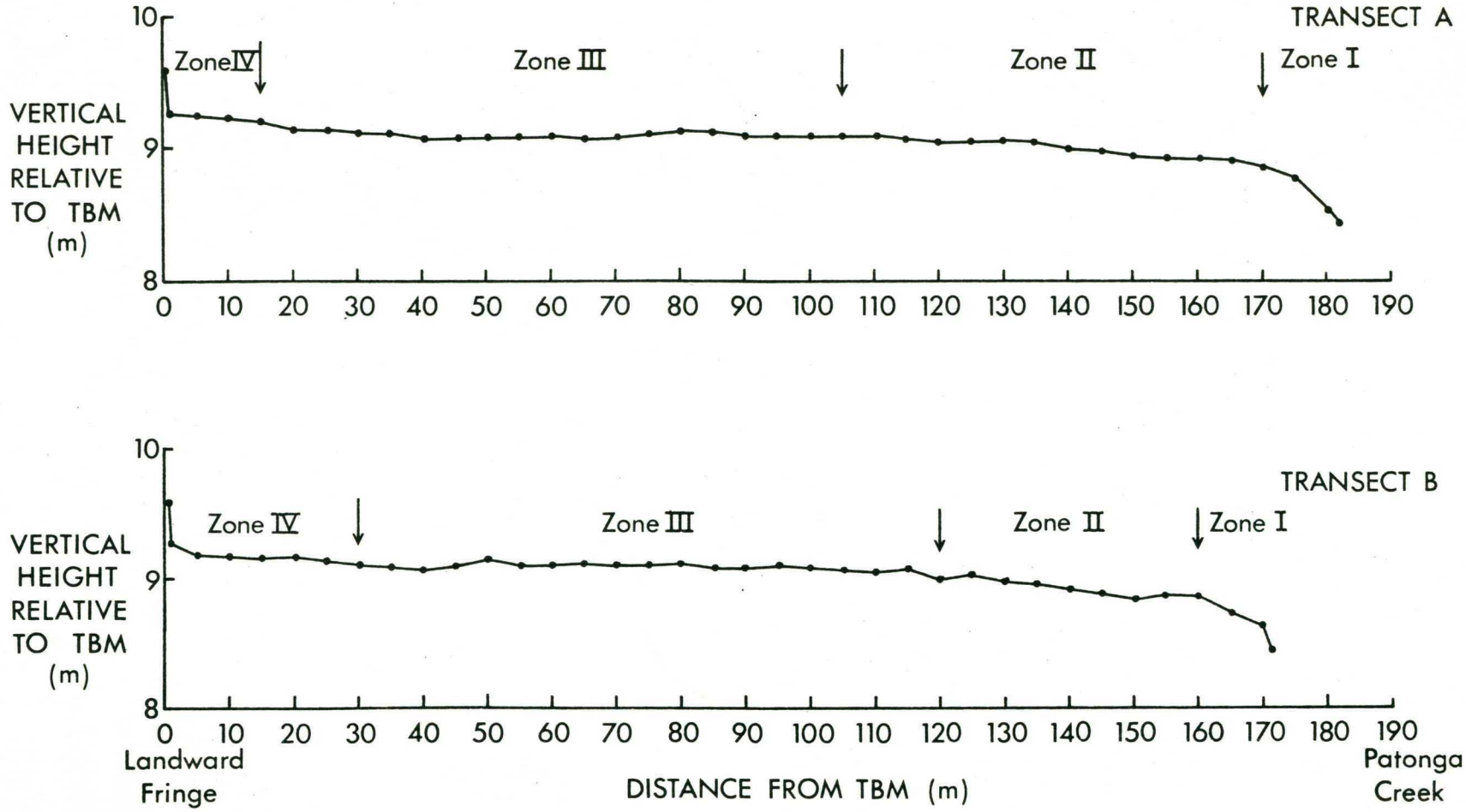

TRANSECT A
Zone IV
Zone III
Zone II
Zone I
VERTICAL HEIGHT RELATIVE TO TBM (m)
10
9
8
0 10 20 30 40 50 60 70 80 90 100 110 120 130 140 150 160 170 180 190
TRANSECT B
Zone IV
Zone III
Zone II
Zone I
VERTICAL HEIGHT RELATIVE TO TBM (m)
10
9
8
0 10 20 30 40 50 60 70 80 90 100 110 120 130 140 150 160 170 180 190
Landward Fringe
DISTANCE FROM TBM (m)
Patonga Creek

TABLE 2-1

Numbers of *Avicennia marina* and *Aegiceras corniculatum* in 50 m^2 quadrats spaced every 5 m along transects A and B.

Distance from back of mangrove swamp (m)	Transect A		Transect B	
	A. marina	*A. corniculatum*	*A. marina*	*A. corniculatum*
0 - 5	0	60+	1	60+
5 - 10	1	60+	2	60+
10 - 15	4	60+	3	60+
15 - 20	3	7	1	60+
20 - 25	2	12	1	60+
25 - 30	1	60+	9	60+
30 - 35	1	52	5	18
35 - 40	4	39	5	10
40 - 45	6	42	4	27
45 - 50	2	22	3	53
50 - 55	1	1	4	20
55 - 60	6	2	3	6
60 - 65	4	0	1	21
65 - 70	5	24	0	16
70 - 75	11	26	3	12
75 - 80	12	60	3	7
80 - 85	2	13	4	11
85 - 90	2	6	3	11
90 - 95	1	15	4	15
95 -100	1	12	4	5
100 -105	2	1	3	4
105 -110	1	0	3	7
110 -115	3	0	2	0
115 -120	2	0	0	2
120 -125	0	0	4	0
125 -130	1	0	0	0
130 -135	3	5	0	0
135 -140	2	0	1	0
140 -145	3	0	1	0
145 -150	0	0	2	0
150 -155	1	0	0	0
155 -160	0	0	1	0
160 -165	0	0	0	0
165 -170	2	0	0	0
170 -175	0	0	0	0
175 -180	0	0	0	0
180 -185	0	0	0	0

2.22 Division of Study Area into Zones

It has been well described (e.g. Watson, 1928; Davis, 1940; Dansereau, 1947; Macnae, 1963, 1966, 1967, 1968; Macnae and Kalk, 1962; Clarkeand Hannon, 1967, 1969; Jones, 1971) that mangrove trees show distinct vertical zonation up a shore and that this is most probably related to factors such as inter-tidal level, salinity of the ground water and drainage of the soil.

It was considered that the distribution of crabs in the Patonga study area might be related to the zonation of the mangrove trees, and this zonation was thus first investigated.

The null hypothesis that mangrove trees Avicennia marina and Aegiceras corniculatum were distributed uniformly over the study area at Patonga in relation to height on the shore was tested.

Materials and Methods

The numbers of each species of mangrove tree were counted in 10 m length quadrats spaced every 5 m along each of the transects A and B. The numbers of trees in 50 m^2 quadrats were thus counted.

Results

Inspection of the data (Table 2-1) indicates that for distances of more than 170 m (transect A) and 160 m (transect B) from the back of the swamp no mangrove trees were present. The area on the lower side of a line joining these two points and down to the junction with the Zostera weed bed was designated

TABLE 2-2

Analysis of variance of numbers of Avicennia marina and Aegiceras corniculatum in Zone II and Zone III (transformed to $\sqrt{\text{number} + 1}$).

Source of variation	Sum of squares	Degrees of freedom	Mean square	F-ratio
Between Zones	4.10	3	1.37	5.11**
Within Zones	14.17	53	0.27	
Total	18.28	56		

Zone III (Transect A)	Zone III (Transect B)	Zone II (Transect A)	Zone III (Transect B)

(In this, and subsequent tables: n.s. denotes non-significance, $P > 0.05$; * denotes significance, $P < 0.05$; ** denotes significance, $P < 0.01$; horizontal lines underlie treatment means which were not significantly different at $P = 0.05$).

Zone I (Fig. 2-4).

Between distances of 105 m and 170 m (transect A) and 120 m and 160 m (transect B) no trees of species A. corniculatum were present. The area bounded by Zone I on the lower side and a line drawn between the 105 m mark (transect A) and 120 m (transect B) was designated Zone II (Fig. 2-4).

Similarly, for distances between 105 m and 15 m (transect A) and 120 m and 30 m (transect B) the species A. corniculatum was present in numbers up to 60 per quadrat. The area bounded by Zone II on the lower side and a line drawn between the 15 m mark (transect A) and 30 m mark (transect B) was designated Zone III (Fig. 2-4).

A single factor analysis of variance (Table 2-2) of the relative numbers of trees of species A. marina along transects A and B in Zones II and III revealed that there was also a significantly greater number of trees of this species in Zone III than in Zone II.

In quadrats at distances less than 15 m (transect A) and 30 m (transect B) from the back of the swamp more than 60 trees of species A. corniculatum were present. The area above a line joining these two points and extending to the back of the swamp at its junction with the terrestrial fringe was designated Zone IV (Fig. 2-4).

Four distinct zones were thus identified corresponding to the relative numbers of each of the two species of mangrove trees present.

FIG. 2-4

Plan of the Patonga study area. Unbroken lines show boundaries between zones; broken lines show survey lines across zones. Rectangles represent areas sampled; letters within rectangles indicate sections of study area (as explained on page 47).

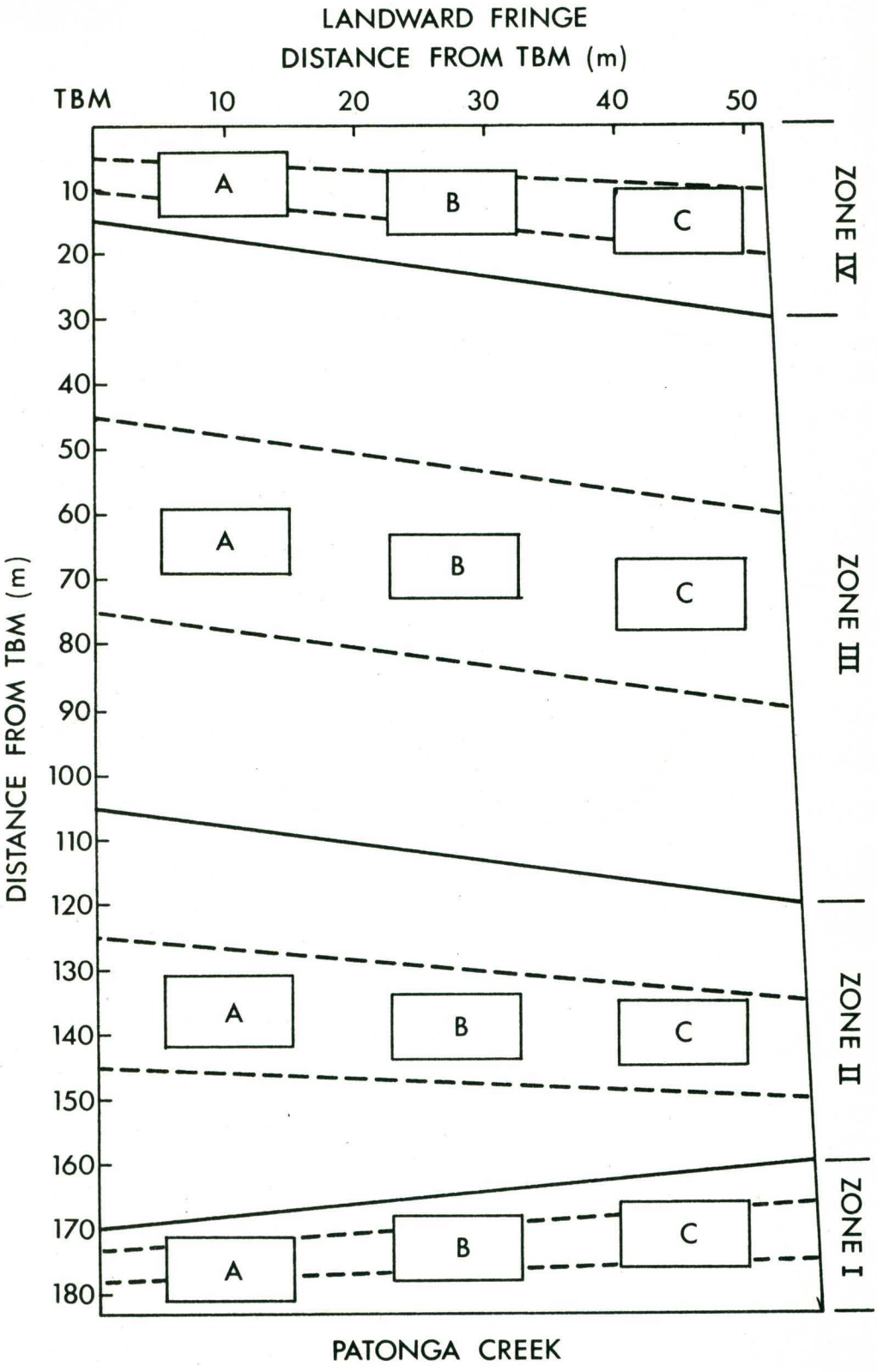

LANDWARD FRINGE
DISTANCE FROM TBM (m)
TBM
10
20
30
40
50
DISTANCE FROM TBM (m)
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
160
170
180
A
B
C
ZONE IV
ZONE III
ZONE II
ZONE I
PATONGA CREEK

TABLE 2-3

Comparison of the number of mangrove saplings in each zone.

A. Mean number of mangrove saplings m^{-2} in each zone

Zone I	Zone II	Zone III	Zone IV
17.6	20.8	25.6	28.0

B. Analysis of variance of numbers of mangrove saplings in each zone

Source of variation	Sum of squares	Degrees of freedom	Mean square	F-ratio
Between Zones	4377.60	3	1459.20	2.58 n.s.
Within Zones	42931.20	76	564.88	
Total	47308.80	79		

TABLE 2-4

Comparison of the number of pneumatophores of Avicennia marina in each zone.

A. Mean number of pneumatophores m^{-2} in each zone

Zone I	Zone II	Zone III	Zone IV
399.2	264.8	233.4	112.0

B. Analysis of variance of numbers of pneumatophores in each zone.

Source of variation	Sum of squares	Degrees of freedom	Mean square	F-ratio
Between Zones	835392.00	3	278464.00	38.01**
Within Zones	556723.20	76	7325.31	
Total	1392115.20	79		

Zone I Zone II Zone III Zone IV

2.23 Survey of Zones

A survey of each zone was conducted to characterise it with respect to numbers of pneumatophores of mangroves, numbers of mangrove saplings and the presence or absence of oysters. A further count of the numbers of mangrove trees in each zone was also made.

Materials and Methods

Two horizontal survey lines were made across each of the four zones, dividing each zone into three equal sections. The species of any mangrove tree one metre on either side of each survey line was noted together with its distance from vertical transect A. This was carried out along each survey line for the first 50 m from vertical transect A.

Further, a 25 cm x 25 cm quadrat was placed on the ground every 5 m along each survey line for the first 50 m from transect A. The numbers of pneumatophores and saplings within the quadrat were counted, and the presence or absence of oysters noted.

Results

The characteristics of each zone are summarised in Fig. 2-5.

There were no significant differences in the mean numbers of mangrove saplings among the four zones (Table 2-3). The mean number of saplings over the study area was 20.8 m^{-2}.

The mean numbers of pneumatophores of mangroves did vary among the zones (Table 2-4). Zone I contained significantly

more pneumatophores (399 m^{-2}) than the other zones; Zone IV significantly fewer (112 m^{-2}). The numbers of pneumatophores in Zone II (265 m^{-2}) and Zone III (233 m^{-2}) did not differ significantly.

Oysters were found on the ground most abundantly in Zone I, while a smaller number was also present in Zone II. No oysters were present in Zones III and IV (Fig. 2-5).

2.24 Discussion

The study area was divided into four zones based on the relative numbers of mangrove trees of each species present. Each zone could also be related to the fall in vertical height from the landward fringe of the swamp.

Zone I (Fig. 2-6) was a 15 m wide strip rising relatively steeply from the Zostera weed bed. It was devoid of mangrove trees, but the ground was covered by the pneumatophores of Avicennia marina and large numbers of oysters.

The presence of A. marina trees characterised Zone II (Fig. 2-7). It stretched from a minimum width of 40 m at the northern end of the study area to a maximum width of 65 m at the southern end. It sloped more gently than Zone I and pneumatophores and oysters occurred in smaller numbers than in Zone I.

The largest zone was Zone III (Fig. 2-8). It was 90 m wide and practically horizontal. It was characterised by the presence of both Avicennia marina and Aegiceras corniculatum in relatively large numbers. Pneumatophores were present, but oysters absent.

FIG. 2-5

Diagrammatic representation of the relative numbers of Avicennia marina, Aegiceras corniculatum, pneumatophores of A. marina, saplings of both species of mangrove tree and oysters in each zone of the study area at Patonga. The mean number of each per m^2 in each zone is shown. This sampling is discussed in Section 2.2.

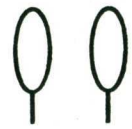
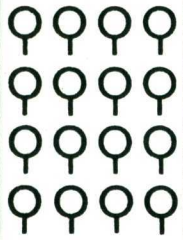
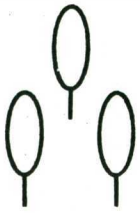
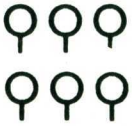
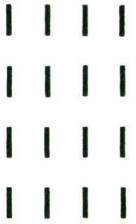
Zone	Avicennia marina	Aegiceras corniculatum	Pneumatophores of A. marina	Saplings	Oysters
IV	 0·05	 1·2 +	 112	 28	
III	 0·07	 0·36	 233	 26	
II	 0·03		 265	 21	
I			 399	 18	

FIG. 2-6

Zone I

FIG. 2-7

Zone II


—trap

FIG. 2-8

Zone III. a, *Avicennia marina*; b, *Aegiceras corniculatum*.


a
b

Zone IV (Fig. 2-9) consisted of a strip of ground ranging in width from 15 m to 30 m, immediately below the terrestrial fringe. It was densely covered by large numbers of A. corniculatum with some A. marina among them. Pneumatophores occurred in relatively small numbers. The ground sloped gently upward towards the terrestrial fringe where there was a sharp vertical rise of about 0.3 m.

The distribution of crabs in the study area was possibly related directly to the zonation of the mangrove trees. This zonation of the mangrove trees was thus used as a basis for devising a programme to sample the population of crabs present in the study area.

FIG. 2-9

Zone IV. A, showing terrestrial fringe at back of study area. B, showing high density of Aegiceras corniculatum.

A

B

SECTION 3 : THE ECOLOGY OF CRABS IN THE MANGROVE SWAMP AT PATONGA.

3.1 INTRODUCTION

Basic to a determination of the relative numbers of crabs and the vertical distribution of crabs on the shore in the study area in the mangroves at Patonga was the development of a sampling programme. The major difficulties in the development of a sampling programme were those encountered in actually capturing crabs: some species are very elusive when on the surface and some species dig very deep burrows from which they are impossible to remove. These two problems have not been solved adequately by other workers in mangrove environments. The techniques of sampling crabs used by other workers are reviewed in Section 3.21; techniques tested in the field in the present study are discussed in Section 3.22.

The sampling programme used in the present study is described in Section 3.3 with the results obtained.

Various physical factors might affect the vertical distribution of crabs on the shore in the study area. These are discussed in Section 3.4, with details of experiments conducted to test their relevance to the distribution of crabs over the study area.

3.2 METHODS OF SAMPLING POPULATIONS OF CRABS

3.21 Review of Methods for Sampling Populations of Crabs.

Various methods have been used by workers in attempts to sample quantitatively populations of crabs in the intertidal zone. The principal factors to be considered in choosing a method are the habits of the crabs and the nature of the particular substratum on which they live. Most methods have involved some type of systematic collection of crabs from the sampling area. Other methods utilized a visual census of crabs or their burrows. The former methods have proved more useful as they allow variables such as the size and sex of individual crabs to be determined. These methods will be discussed first.

Teal (1958) sampled crabs of the genus Uca in salt marshes in Georgia. He placed iron cylinders of 0.2 m^2 cross-sectional area over the marsh at high tide. During high tide, the animals were in their burrows or at least not grouped together in herds. At low tide, Teal dug out the soil enclosed in each iron ring and removed the crabs. The iron cylinders were placed in the mud to a depth of 30 cm, so that they extended below the maximum depth to which the crabs burrowed. The maximum density recorded by Teal was 61 crabs m^{-2}.

Ono (1962, 1965) sampled various species of the family Ocypodidae in a mixed substratum which varied from sandy to muddy and silty along the coast of Kyushu, Japan. Ono counted the positions of burrows in 1 x 1 m^2 quadrats which had previously been mapped. He then collected individual crabs in 50 x 50 cm^2

quadrats set on the corners of the larger quadrats. Individual crabs were collected by digging by hand in the muddy areas and by sieving in the more sandy areas. In later experiments Ono set up field cages to a maximum depth of 12 cm, indicating that this was the maximum depth of burrows of the crabs he was sampling. The maximum number caught was 40 m^{-2}.

In a study of the distribution of crabs in a Jamaican mangrove swamp, Warner (1969) marked out five 1 x 1 m^2 quadrats in each zone being sampled. He then dug the crabs out of the mud by hand and collected them from the trees above each quadrat. Warner commented, however, that "not all species could be conveniently sampled in this way. It was often impossible to extract adult Uca species and Ucides cordatus from the burrows because of the tangle of the mangrove roots under the mud." In an effort to estimate relative numbers of these species the burrows of all species were counted in each quadrat before searching commenced, and large collections of Uca species from the five zones were later used to determine relative numbers of each species in each zone. Warner, however, cast doubt on the use of counts of burrows for the estimation of abundance. He referred to the following two types of associations:

"(i) in which individual crabs made use of burrows constructed and occupied by a member of a different species, and

(ii) in which several crabs of several species inhabited an anastomising system of tunnels just under the swamp floor and not apparently constructed by any individual or species in particular."

One species, Goniopsis cruentata, which did not dig burrows and was too fast to be caught by hand, was recorded qualitatively by noting the number seen in each zone on each sampling occasion. "The other crabs are relatively small and do not burrow deeply and were easily captured within the quadrats." The maximum density of crabs sampled by the above methods was 16 m^{-2} for the species Aratus pisoni.

The methods used by Griffin (1971) to estimate the relative numbers of species of crabs of the families Grapsidae and Ocypodidae on the south-east coast of Tasmania were random searching for periods of 10, 20 or 60 minutes and collection by hand of all crabs in quadrats of sizes 1 m^2 or 16 m^2. The exact method adopted depended on the locality, which ranged from rock platforms to stony and boulder beaches. None of these areas supported mangroves. The maximum density recorded was 149 m^{-2} for Cyclograpsus granulosus.

Sasekumar (1974), in sampling the total infauna in the soil of a Malayan mangrove swamp, dug out and collected the crabs from 0.11 m^2 areas with a spade to a depth of 20 cm. He was not able to sample the large decapods whose burrows reached greater depths. The maximum density of crabs sampled in this way was 140 m^{-2} for Upogebia species.

Similar methods were used by Frith et al., (1976) in sampling total infauna in a mangrove swamp in Thailand. They placed 0.5 m^2 quadrats at each sampling point and collected animals on the surface by hand. They then dug up soil within the quadrat to a depth of 25 cm and removed all animals that

were visible. The maximum density of crabs sampled in this way was 19.2 m^{-2} for Uca lactea annulipes. Frith et al., also commented that they could not sample accurately those large crabs that burrowed below 25 cm.

In sampling the infauna of the mangrove and salt-marshes of Careel Bay, New South Wales, Hutchings and Recher (1974) used spades to dig out 9000 cm^3 samples of the substratum. These were then sieved to extricate the animals. This was done to a depth of only 10-20 cm and "the deep burrowing animals were probably missed or underestimated by this method." Separate observations carried out at night at low tide while the animals were feeding indicated numbers of crabs as follows: Paragrapsus laevis - 24 - 30 m^{-2}; Sesarma erythrodactyla - 13 - 88 m^{-2}; Heloecius cordiformis - 3m^{-2}; Australoplax tridentata - 9 m^{-2}. Similar counts during the day at low tide were reported to be in the order of 10 - 15 m^{-2}.

Visual censuses of the inhabitants on the floor of a mangrove swamp were made by Golley et al. (1962) in Puerto Rico. 1 x 1 m^2 quadrats were placed on the floor of the swamp at low tide and an observer sat motionless beside the plot for one hour recording all animals seen and noting the time each spent on the plot. This was done at night and during the day. As different species were active at different times, the census during the time of maximum activity was used to calculate densities. The maximum density calculated was 5 m^{-2} for Uca mordax.

Berry (1963), in a study of faunal zonation in a Malayan mangrove swamp, observed many crab species, but the only ones he attempted to sample quantitatively were various species of

Uca. He sampled these by counting the number of burrows of Uca in 0.11 m^2 areas. This gave a maximum number of 21 m^{-2}.

Frey et al. (1973) reviewed techniques available for sampling the benthos of salt-marshes, particularly for sampling burrowing animals. They recognised that capture-recapture techniques were unsatisfactory for sampling populations of crabs on a large scale because:

"(i) paints and other markings are frequently too ephemeral, due to the animals' burrowing habits;

(ii) commotions raised by the pursuit, capture and release of crabs induce considerable small-scale migration, essentially damping the data for a specific sampling site; and

(iii) certain species of crabs are too secretive and/or too sparse locally to be found and tagged in significant quantities by a person walking through the marsh."

They also concluded that counts of types and densities of burrows were inaccurate because:

"(i) burrows excavated by different species of crabs are not always distinguishable;

(ii) previous domiciles may be abandoned and new ones constructed; and

(iii) among certain species, more than one individual may occupy a given burrow."

Frey et al., (1973) also recognised that some crabs did not actually construct burrows.

A method of counting the animals within a high-walled quadrat tossed onto the marsh surface also failed. The frames

were either "too heavy to be thrown the distances necessary to capture an undisturbed group of animals, or too light to press down the marsh grass far enough to seal the base of the quadrat to the marsh surface."

Frey et al. (1973) concluded that the most successful method of sampling was to secure high-walled quadrats with wooden frames (1 x 1 m^2 x 20 cm high) to the surface of the marsh while some water still covered the marsh. Crabs could then be collected from within the quadrat when they came to the surface as the water receded. Most crabs could be collected from within a quadrat in this way, especially if the area was left at regular intervals to allow any remaining animals to return to the surface undisturbed by the collector, who could catch them when he returned. This method required approximately one hour spent per m^2 searched. Wolf and Fanning (1970), in sampling crabs of the genus Uca, in a salt-marsh in Georgia, evaluated the increased recovery obtained by digging up the quadrat after sampling was finished. Any unsampled crabs could then be found. They concluded that the increase in accuracy of the sample did not warrant the extra work involved.

Whilst various methods of sampling crabs have been employed in different environments, it is apparent from the above discussion that none of these has been successful in sampling the deep burrowing crab species in a mangrove swamp. The depth of the burrows, the elusiveness of the crabs and the nature of the substratum make this a difficult task.

3.22 Comparison of Methods of Sampling Populations of Crabs tested in the Present Study.

Numerous sampling methods were considered and tested in the present study before the final sampling procedures were chosen. Some of the methods tested were modified from those used by other workers in mangrove and non-mangrove environments, as discussed in the previous section. Some other techniques had not previously been used. Each technique is outlined below, together with the results of trials in which it was used, and a discussion of its suitability for the present study.

3.221 Collection of crabs on the surface.

As the tide receded 1 m x 1 m quadrats were marked out on the surface and surrounded by 15 cm high walls of galvanised iron. They were left undisturbed until the area was completely emersed and maximum emergence of crabs from their burrows had taken place. Then, as quickly and quietly as possible, crabs were collected by hand. Attempts were also made to remove from their burrows crabs that had not emerged but could be seen in the entrance of a burrow and to collect crabs that had retreated to their burrows as the collector approached (Fig. 3-1A).

This method of sampling proved unsatisfactory for the following reasons.

(i) Because of the high density of the mangrove Aegiceras corniculatum in Zone IV (Table 2-1, Fig. 2-5) it was:

(a) impossible to place the high-walled quadrats in position without biasing their placement to those areas of

FIG. 3-1

A. Quadrat surrounded by galvanised iron walls; funnel traps set in soil.

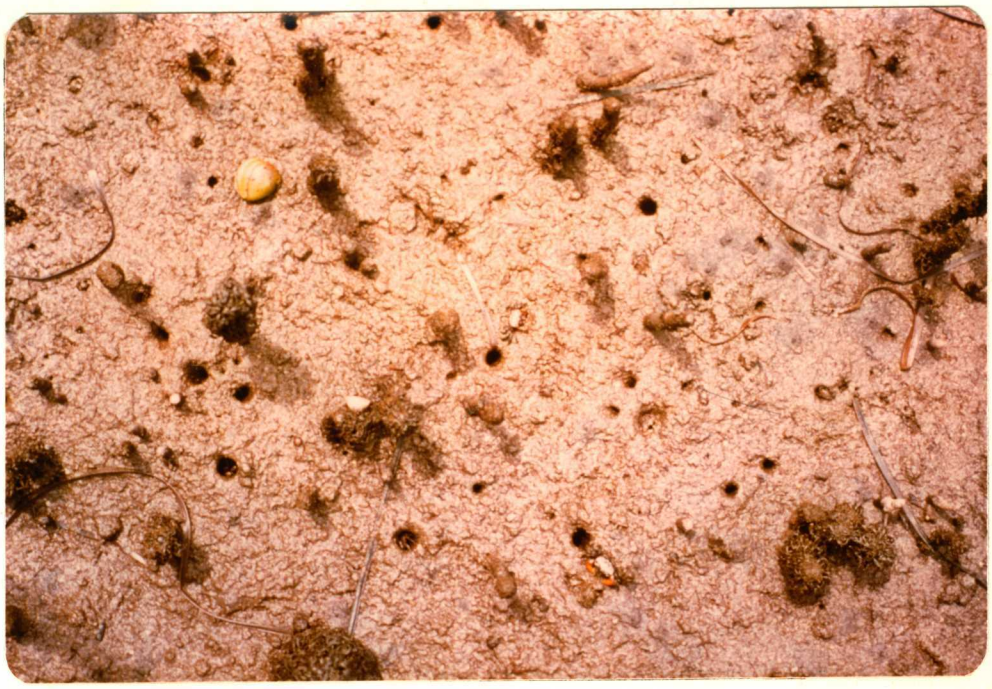
A

FIG. 3-1 (cont.)

B. Burrows of *Heloecius cordiformis* and *Australoplax tridentata*.

C. Entrance to a large burrow of *Sesarma erythrodactyla*. Smaller burrows of *H. cordiformis* can also be seen.

B



C

lower density of trees within this zone; and

(b) impossible to move among the trees sufficiently quickly to catch crabs on the surface.

(ii) This method depended on the emergence of crabs on the surface during daylight hours at low tide. Heloecius cordiformis, Australoplax tridentata and, to a lesser extent, Sesarma erythrodactyla, were active on the surface during the day, particularly during the summer months. Very few Paragrapsus laevis, however, were seen out of burrows on the surface during the entire period of the study. Hutchings and Recher (1974) at Careel Bay, N.S.W., also reported small numbers of P. laevis on the surface during the day, and considerably larger numbers at night.

(iii) The crabs moved quickly over the surface of the soil as soon as the collector approached a quadrat. Many crabs disappeared into burrows, regardless of whether or not they were the "owners" of a particular burrow. S. erythrodactyla moved very quickly and sought shelter beneath pieces of fallen timber. These were usually lying in depressions in the substratum and filled with muddy water, which concealed any entrances to burrows. In Zone I, crabs could quickly dig into the soft mud or seek refuge among the oysters. Collection of adequate numbers and unbiased samples from the surface was thus not possible, even when the quadrat was left undisturbed at regular intervals during the collection to allow remaining animals to reappear on the surface before the collector returned.

(iv) Once the crabs had reached their burrows then the task of capturing them was much more difficult. H. cordiformis

and A. tridentata dig vertical, unbranching burrows (Griffin, 1968) and were the easiest species to capture (Fig. 3-1). However, if they were not caught near the mouth of the burrow, and a trowel or spade not used to seal off the burrow below, their capture proved almost impossible. The matted roots and pneumatophores of the mangroves in the tightly-packed soil made digging difficult. The muddy water which filled the hole made it impossible to see the extent of the burrow, the presence of crabs or to judge the depth to which it had been dug. The presence of oysters, among which the crabs soon disappeared when disturbed, and the high moisture content of the soil were further difficulties which made recovery even harder in Zone I.

P. laevis and S. erythrodactyla were the most difficult crabs to remove from their burrows. The burrows were deep, extensive and formed a horizontally branching network (Fig. 3-1). Attempts to trace burrows and dig out the crabs of those two species were unsuccessful. The "anastomising system of burrows and crab runs" described by Warner (1969) was also found in the present study.

Attempts were made not only to trace burrows and establish their depth and shape by digging, but also to make casts of them using a fast-setting cement mixture (Sellys Speed Cement, Sellys Chemical Co., Bankstown, N.S.W.). This proved unsuccessful because the cement quickly spread into the moisture of the surrounding burrow walls before setting. The size and branching of the grapsid burrows made it impractical to fill an entire burrow or network of burrows. The use of polyester plastic and hardener to make burrow casts as described by Frey et al. (1973) was

beyond the scope of the present study.

Collection of crabs on the surface, by hand, thus proved to be an inadequate method of sampling P. laevis and S. erythrodactyla, and had only very limited value for H. cordiformis and A. tridentata.

3.222 Collection of crabs by digging.

High-walled 1 m x 1 m quadrats were laid out on the soil surface as the tide ebbed, as described in the previous section. All crabs which could be caught by hand on the surface were collected. The soil in the entire quadrat was then dug out to a depth of 20 cm. Crabs were separated from the soil by hand, or after passing the soil through a large sieve. This method proved unsatisfactory because of the small number of crabs caught and because of the impracticality of digging in the mangrove environment.

The low recovery of crabs principally resulted from the fact that the burrows of most of the crabs extended below a depth of 20 cm. When the quadrat was approached, the crabs retreated into burrows and went below this depth.

The removal of soil from the quadrats proved impractical because of the difficulty of digging into the tightly-packed soil and matted mangrove roots and pneumatophores in each zone. Digging was especially difficult among the oysters in Zone I and the roots of the closely packed Aegiceras corniculatum in Zone IV. The judgement of the exact depth to which the soil had been removed was also difficult, particularly in Zone I, because of the muddy

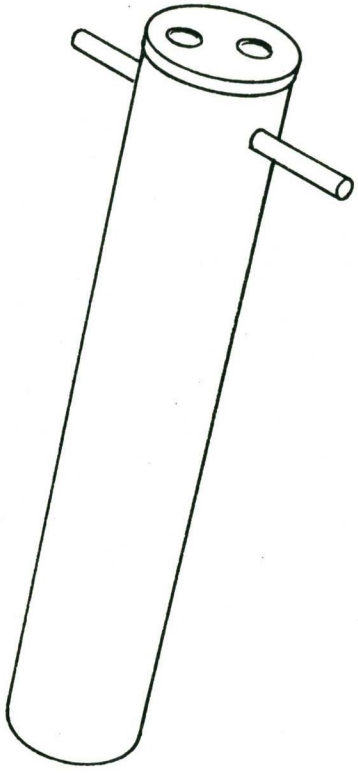


FIG. 3-2 CORE – SAMPLER ($\times \frac{1}{10}$)

water which filled the hole as soon as a spade-full of soil was removed.

Subsequent separation of crabs from the soil and tangled roots, by hand, was both difficult and time-consuming. Sieving was necessary, and as this involved either pumping water into each zone to wash through the sieve or else transporting all the soil removed from each zone to the water's edge, it was considered impractical, especially in view of the large volume of soil to be handled. Frith *et al.* (1976), in their study of a mangrove swamp in Thailand, commented on the impossibility of sieving muddy soil *in situ* and the impracticality of returning large quantities of soil to the laboratory to sieve.

Digging out the crabs was thus considered unsuitable for the present study, because of the time-consuming nature of the physical work involved, and the small number of crabs which could thereby be collected. Digging also caused detrimental disturbances to an area, making it difficult to be able to sample in the same localities at monthly intervals.

3.223 Collection of crabs using a core-sampler.

A cylindrical metal tube (Fig. 3-2), open at the bottom and covered at the top by a metal plate with two small holes in it, was dug into the soil to a predetermined depth. Rubber stoppers were inserted into the two holes in the top to form an airtight seal. The corer was then removed together with the enclosed core of soil. This procedure was repeated a set number of times in each zone at low tide and the crabs separated from the cores of soil. Two such corers, of 10 cm

and 15 cm diameter, respectively, and 1 m long, were made and tested in the field.

In the trials conducted, the maximum number of crabs caught in the larger sampler was 3 crabs per core. Thus, collection of sufficiently large samples necessitated many cores in each zone.

As with the previous methods difficulties were encountered in pushing the corer among the roots and pneumatophores, the closely-packed Aegiceras corniculatum in Zone IV and the oysters in Zone I. Because of the loose consistency of the soil in Zone I, it was particularly difficult to lift the core of soil up with the corer. The soil fell out of the bottom of the corer as soon as it was lifted clear of the surface.

The choice of a uniform depth of cores was influenced by variations in the texture of the substratum. The greatest limitation was caused by the closely-packed roots through which the corer had to be pushed, particularly in Zone IV. In contrast, depths of up to 60 cm could be reached, especially in Zones I and II. On some occasions, however, crab burrows were seen to extend deeper than this.

Once the cores had been taken, the crabs had to be separated from them. The difficulties encountered in separating crabs from the soil have already been discussed in the previous section. Thus, considering the great amount of time and effort needed to obtain sufficient numbers of any of the species being sampled, this method was considered unsuitable for the present study.

3.224 Capture, mark and recapture.

Capture, mark and recapture techniques (e.g. Smith, 1966) were considered for estimating densities of populations of crabs in the present study. They were judged unsuitable for the following reasons.

(i) As previously discussed (in section 3.221) systematic capture of crabs on the surface or from burrows was unsuccessful.

(ii) A satisfactory method of marking crabs could not easily be found.

(iii) Such a sampling programme would require very frequent and regular visits to the sampling area, and this was not possible in the present study.

(iv) Those difficulties found by Frey *et al*. (1973), and discussed in section 3.21, would have had to be overcome.

3.225 Use of Chemical Agents to Remove Crabs from Burrows.

The possible use of pouring a dilute solution of quinaldene (Muench, 1958) into crab burrows as a method of forcing crabs to come to the surface was investigated. If successful, such a method can be used following collection by hand of crabs on the surface within 1 m x 1 m marked quadrats. Quinaldene would allow extraction from their burrows of those crabs that could not be caught on the surface. This method was tested but with poor results. From a total of 20 burrows into which quinaldene was poured, only two crabs emerged onto the surface. In all other cases, even though it was known that there was a crab in

the burrow, no crab appeared on the surface.

The chief problems with the use of solutions of chemicals to extricate crabs from their burrows, in addition to the low recovery rate, were as follows.

(i) As has been previously described many of the crab burrows were deep and branched extensively and very large volumes of solution would be required.

(ii) The solution of quinaldene diffused into the water in the burrow walls and at the bottom of the burrow was quickly diluted.

(iii) Little is known about the effects of differing concentrations of chemicals such as quinaldene on crabs. It is possible that rather than driving the crabs from their burrows they may have been killed or anaesthetised and remained at the bottom of the burrow. Large scale tests would have been required to find not only the best chemical agent to use but also, if at all effective, the concentration which caused maximal numbers of crabs to emerge.

(iv) The effects of pouring large volumes of such chemicals into the mangrove swamp, especially the effects on other animals and plants, would obviously have needed investigation before it could be used on the large scale needed in this study.

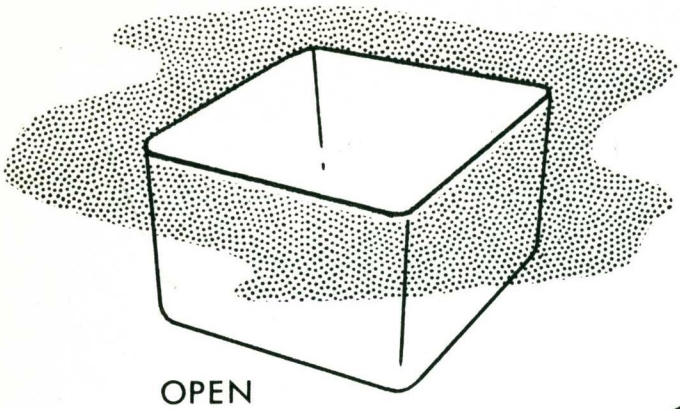
Thus, the use of chemical agents to extricate crabs from their burrows was not considered further.

3.226 Trapping

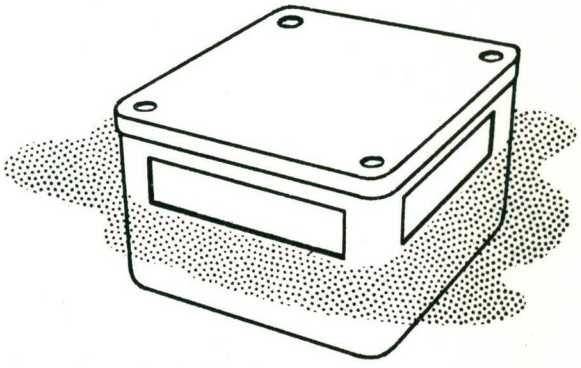
Trapping is widely used in the sampling of vertebrates (Taber and Cowan, 1969; Overton and Davis, 1969; Flowerdew, 1976), but has not often been used in the case of invertebrates, except for catching crabs and lobsters by commercial fisheries. It was considered that pitfall traps, set in the soil for a period of time at low tide, might be successful in catching sufficiently large numbers of crabs for sampling purposes. Various kinds of traps, with and without baits, were tested.

In the first series of trials, conducted to determine suitable baits, samples of baits were laid out on the mud surface during daylight as the tide ebbed and observed from a distance through binoculars. Observations were made for two hours before low tide and two hours after low tide. Any crab that approached or fed on the baits was noted. Baits used were household scraps (bacon fat, vegetable scraps), fresh mullet, mullet gut and sardine (from tins of sardine in sardine oil). On the two occasions such tests were conducted only a solitary H. cordiformis was seen to approach the baits. It quickly moved past them and showed no further interest in them. No other crabs approached the baits. Either the baits were not attractive to the crabs, or the crabs would not feed during daylight. Consequently, the baits were tested in traps which were left in position in the soil for 24 hours. The baits were therefore available to the crabs at both high and low tide, in darkness and daylight.

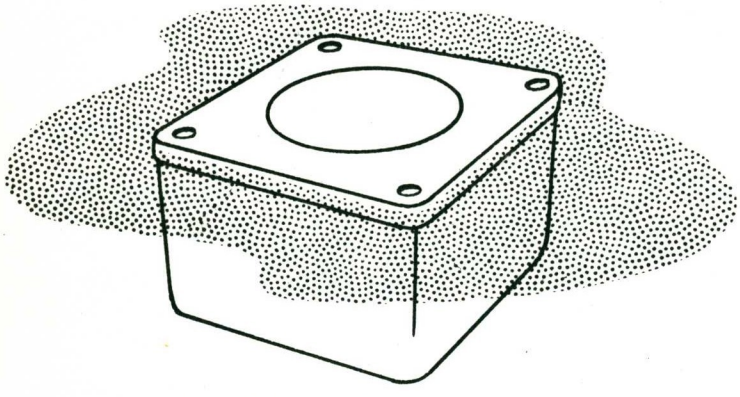
The traps that were tested are illustrated in Fig. 3-3 and described below.



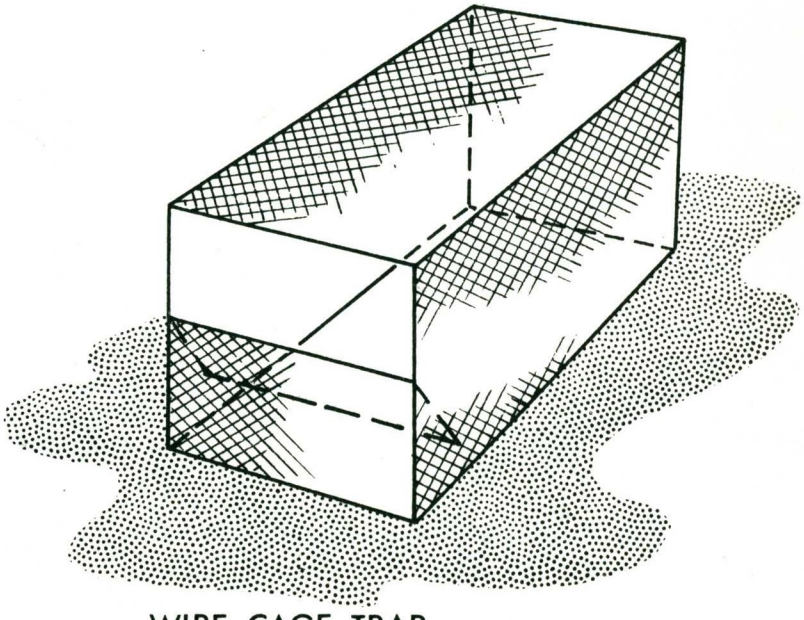
OPEN
PITFALL TRAP



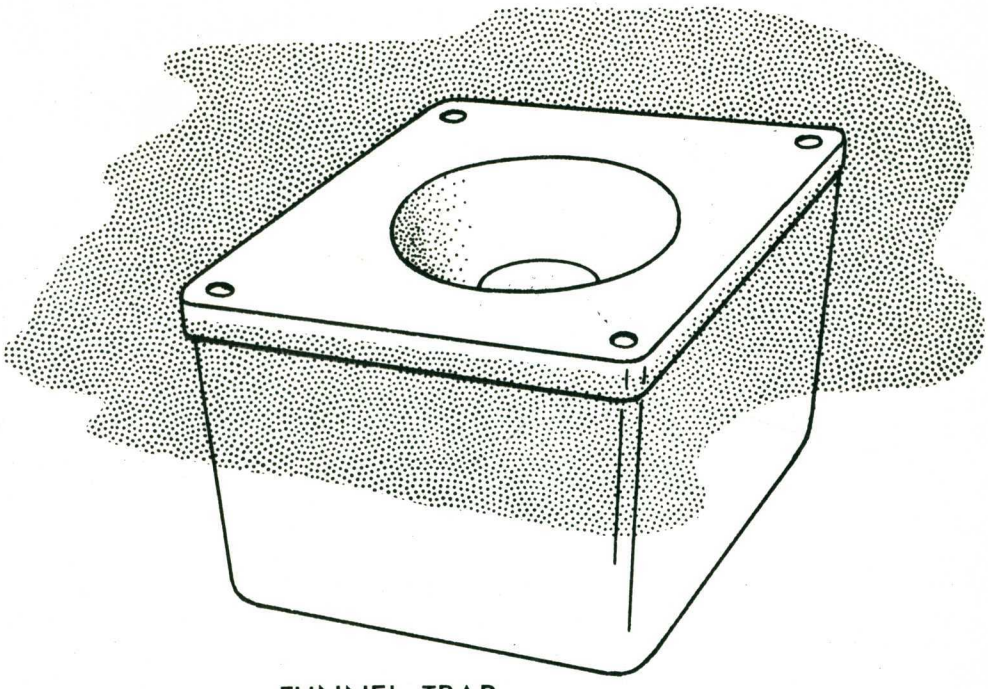
WINDOW TRAP



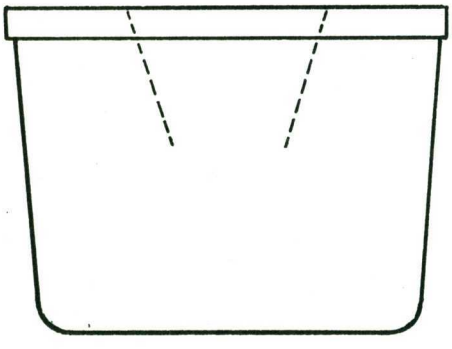
ROOF TRAP



WIRE CAGE TRAP



FUNNEL TRAP



SIDE VIEW OF FUNNEL TRAP

FIG. 3-3 TRAPS TESTED FOR SAMPLING CRABS

TABLE 3-1

Results of preliminary trapping experiment 1

(conducted July, 1974)

Type of trap	Number of traps	Species of crab	Total number of crabs caught	Mean number of crabs per trap
Open pit-fall	12	*S. erythrodactyla*	4	0.3
		P. laevis	4	0.3
Window	8	*S. erythrodactyla*	7	0.9
		H. haswellianus	2	0.3
Roof	7	*S. erythrodactyla*	2	0.3
		P. laevis	3	0.4
		H. haswellianus	1	0.1
Wire cage	6	*P. laevis*	1	0.2
Funnel	6	*S. erythrodactyla*	9	1.5
		P. laevis	17	2.8

(i) Open pitfall trap. A plastic container (2 litre ice cream container), 170 mm square and 100 mm deep, was set in a hole in the mud with the top level with the soil surface. Four small holes of 5 mm diameter were punched in the bottom of the container to ensure that it would not be pushed out of the ground by the water of the incoming tide.

(ii) Window trap. Rectangular windows, 25 mm x 80 mm, were cut out of each of the four sides of a plastic container, 10 mm from the top of each side, and the trap set to a depth of 65 mm into the mud with the bottom edge of each window level with the soil surface. A lid was placed over the trap. Four small holes were punched in the lid as well as in the bottom of the trap, in similar fashion to that described above, to ensure that the incoming tide would not dislodge the trap.

(iii) Roof trap. A plastic container with a lid was buried in the soil to the level of the lid. A hole of 100 mm diameter was cut in the lid to provide an entrance for the crabs. Small holes were punched in the bottom and lid of the trap, as previously described.

(iv) Funnel trap. These were identical to the roof trap but with the addition of a section of a plastic funnel which was glued to the inside of the lid around the opening. The funnel was 100 mm in diameter at the lid of the trap and decreased to 50 mm diameter at its bottom, which was 50 mm below the inner surface of the lid. These were buried in the soil to the level of the lid (Fig. 3-1A).

(v) Wire cage traps. A wire framework, 250 mm x 150 mm x 130 mm, was covered in a wire mesh, except for a 150 mm x 60 mm

TABLE 3-2

Results of preliminary trapping experiment 2.

(conducted July, 1974)

Trial Number	Number of traps	Species of crab	Total number of crabs caught	Mean number of crabs per trap
1	5	*P. laevis*	20	4.0
2	3	*P. laevis*	6	2.0
		S. erythrodactyla	1	0.3
3	3	*P. laevis*	8	2.7
4	7	*P. laevis*	27	3.9
		S. erythrodactyla	6	0.9
		P. serratifrons	1	0.1

entrance at one end. The entrance had a flap of wire mesh which hung down inside the trap to hinder escape of crabs. The trap was placed on the surface of the mud and held in place by metal stakes.

In the first trials traps of each kind were placed in position in the mud in Zone II at low tide. Crabs were collected from the traps at low tide on the following day. Each type of trap was tested unbaited and then baited with each of the baits previously listed. The mean number of crabs caught per trap in unbaited traps and in those baited with household scraps, pieces of mullet or mullet gut was less than 1 per trap.

A summary of the results obtained for each kind of trap when baited with pieces of sardine is contained in Table 3-1. The funnel trap was the only type which caught greater numbers of crabs than a mean of 1 per trap. The mean number of Sesarma erythrodactyla was 1.5 per trap and that of Paragrapsus laevis was 2.8 per trap. Other species were not caught in such great numbers. While crabs were probably attracted equally to all traps, the restricted chances of escape from the funnel trap were most certainly the reason for its greater success.

A further four trials with funnel traps baited with sardine and placed in Zone II yielded mean numbers of P. laevis ranging up to a maximum of 4 per trap and S. erythrodactyla up to 0.9 per trap (Table 3-2).

Three trials in which funnel traps (baited with sardine) were placed in three or four of the zones were then conducted. The results confirmed the usefulness of funnel traps for sampling

TABLE 3-3

Results of preliminary trapping experiment 3.

(conducted July/August, 1974)

Trial Number	Species of crab	Mean number of crabs per trap			
		Zone I	Zone II	Zone III	Zone IV
1	S. erythrodactyla	0.6	0.6		1.0
	P. laevis	1.3	2.0		0
	H. haswellianus	0	0		1.3
	P. serratifrons	0.1	0		0
	I. paludicola	1.0	0		0
	(Number of traps	9	5		8)
2	S. erythrodactyla	0.3	0.4		1.0
	P. laevis	1.4	0.8		0.1
	H. haswellianus	0	0		0.6
	H. cordiformis	0.2	0		0
	A. tridentata	0.3	0		0
	I. paludicola	2.4	0		0
	(Number of traps	9	5		9)
3	S. erythrodactyla	1.0	2.2	2.4	0.3
	P. laevis	3.1	2.9	2.9	0
	H. haswellianus	0	0	0	0
	H. cordiformis	0.2	0	0.2	0
	A. tridentata	0.1	0	0	0
	I. paludicola	0.6	0	0	0
	P. serratifrons	0.4	0	0	0
	(Number of traps	10	10	10	10)

S. erythrodactyla and P. laevis, and indicated as well their possible use in providing information on some of the less abundant species (Table 3-3). Ilyograpsus paludicola (see comments on this species in Section 1,p.3) and Helograpsus haswellianus were not, in fact, detected in the mangroves at Patonga until they appeared in traps during this series of trials. These species were apparently restricted to Zones I and IV respectively. On the other hand, the numbers of Heloecius cordiformis and Australoplax tridentata caught in traps were very small and of little use for comparison of relative numbers among the four zones.

3.227 Counts of burrows

Comparison of the numbers of burrows of each species of crab in each of the four zones was considered unsuitable as a method of estimating numbers of crabs for the reasons discussed below.

(i) In many places crabs were seen to disappear into the mud, yet no distinct burrows were present. This occurred principally in the following two cases.

(a) In the lower parts of Zone I, even at low tide, the mud was not sufficiently hard to support burrow walls and crabs were seen to dig into the mud or disappear among the oysters leaving no distinct burrow entrance behind them. Samples collected for the study of the reproductive biology of P. laevis (Section 4) were nearly all collected from among the oysters in Zone I in an area adjacent to the study area. This was the only reliable place to catch crabs of this species on the surface, yet no burrows were seen.

(b) Many S. erythrodactyla were seen to run into depressions in the soil which were filled with muddy water, and were often beneath pieces of fallen timber. The crabs disappeared from sight down burrows with concealed entrances. It was not possible to count these burrows. In many cases it was not possible to determine whether distinct burrows were, in fact, present or whether the crabs had just dug down into the soft soil in the depression, which was possibly too wet to support burrow walls.

Each of the above cases would lead to a marked underestimate of the number of crabs present. The first, being confined to Zone I, would make comparison with the other zones difficult.

(ii) Even when distinct burrows were present, identification of the species of crab to which each belonged was unreliable. Difficulties arose in the following instances.

(a) Many of the burrows of small H. cordiformis and A. tridentata appeared similar, as did those of large H. cordiformis and small S. erythrodactyla.

(b) P. laevis were rarely seen in burrows and the large burrows thought to be constructed by them were often seen to contain S. erythrodactyla. Whether these burrows were built by P. laevis and only used by S. erythrodactyla when escaping the collector, whether they were shared with S. erythrodactyla, or whether they were built and occupied only by S. erythrodactyla remained unclear (Fig. 3-1). Because of the size and extensiveness of the larger burrows of S. erythrodactyla and P. laevis, it seemed probable, however, that, at least for these species, there was a complex system of tunnels occupied by groups of crabs.

Each system of tunnels probably had more than one opening. It was impossible to determine any relationship between the number of openings and the number of crabs in a system of burrows.

(iii) As has been previously mentioned, burrows were often excavated but were found to contain no crabs. Apart from the difficulties of tracing the burrows, it is probable that some of the burrows were in fact unoccupied, the owners having dug more than one burrow. In experiments in tanks in the laboratory, Griffin (1971) found that H. cordiformis constructed "many more burrows than were finally occupied." Experiments conducted in the present study (Section 3.4) confirmed this observation. Again, any relationship between the number of burrows dug and the number of crabs was not known.

3.228 Visual census.

Golley (1962) conducted a visual census of crabs in a Puerto Rican mangrove swamp (see Section 3.21). Observers sat beside 1 m x 1 m quadrats for periods of 1 hour and recorded all the animals seen. Without a team of observers to observe quadrats in each zone simultaneously at low tide, this method is extremely time consuming. As the present study was conducted by the author alone, such a method was totally impractical.

Other difficulties associated with the use of a visual census were as follows.

(i) It was difficult to observe crabs among the densely tree-covered areas of Zone IV and among the fallen timber and oysters in other zones.

(ii) Only small numbers of all species, except H. cordiformis in the summer months, were visible on the surface in a 1 m x 1 m quadrat during a 1 hour period. Together with the almost complete absence of P. laevis on the surface during daylight, this made it impossible to compare relative numbers of crabs in each zone, unless a large number of quadrats could be observed.

(iii) An accurate count of the large numbers of H. cordiformis in some zones was difficult, particularly because they moved about rapidly over the surface. Further difficulties were caused by the behaviour of many of the crabs. Individuals emerged on the surface, disappeared down a burrow for some time, and then re-emerged on the surface, making it difficult to count them (Griffin, 1968).

3.229 Photographic census

The observation of quadrats as described in the previous section was generally of little use in sampling most species. It was, however, considered that some kind of visual census could be successful, for counting H. cordiformis, because large numbers of this species were visible during the day. A camera was mounted on a fixed tripod about 1 m high and focussed on a 0.25 m^2 area of the substratum. It was left undisturbed for 5 minutes and the shutter then closed using a 6 m long

extension release. Trials using this method indicated that many H. cordiformis re-emerged onto the surface within five minutes after placing the camera in position. The numbers of crabs were sufficient for a comparison of relative densities of H. cordiformis in the four zones.

3.3 SAMPLING OF THE POPULATION OF CRABS IN THE PATONGA MANGROVES.

3.31 Introduction

It is apparent from the previous section that no single method can be successful for sampling all the species of crabs present in the Patonga mangroves in sufficient numbers to allow determination of distribution among the four zones or any changes in this over a twelve month period. A sampling programme was therefore devised that concentrated on the most abundant species of crabs present (*Sesarma erythrodactyla*, *Paragrapsus laevis* and *Heloecius cordiformis*), and would also yield some information on the less abundant species.

The sampling programme was designed to test the null hypotheses that the species of crabs in the study site at Patonga mangroves were evenly distributed over the four zones, and that this distribution did not change during a twelve month period. The two following sampling techniques were used:

(i) trapping of crabs in baited pitfall traps; these were primarily designed to sample *S. erythrodactyla* and *P. laevis*, and

(ii) photographic census of crabs from slides taken while crabs were out of their burrows on the surface of the mud; this was primarily designed to sample *H. cordiformis*.

3.32 Trapping

Materials and Methods

Trap samples were taken monthly from September, 1974, to November, 1975, with the exception of August, 1975. On each occasion, each of the four zones within the study area was sampled. To ensure that individual sites were not sampled too frequently, the study area was further divided into three sections (A, B and C) horizontally along the shore (Fig. 2-4) and these were sampled in sequence beginning with section A in September, 1974. Each section was thus sampled once every three months.

At each time of sampling 10 funnel traps (Section 3.226; Fig. 3-3) were placed in the centre of each zone in the section to be sampled. The traps were placed in two rows spaced 10 m apart; each row contained 5 traps spaced at 5 m intervals. All 40 traps were placed in the mud at low tide on one day and the crabs collected on the following day. The traps were each baited with a piece of sardine, about 3 cm long, covered with sardine oil. The bait was enclosed in a 6 cm^2 bag of nylon flyscreen mesh which was sealed with metal staples to prevent removal of the bait by crabs.

Each trap was placed in a hole with its top level with the surface of the mud (Fig. 2-6). Mud was pressed around the sides of the trap to prevent its dislodgement by water movement as the tide rose and fell.

The following data were recorded for each crab from each trap:

(i) species,

(ii) sex,

(iii) maximum carapace width,

(iv) whether or not female crabs were gravid (carrying eggs externally beneath the abdomen), and,

(v) any unusual or interesting observations on individual crabs.

The crabs from each trap were then released at the site of capture. The trap was removed and its hole filled in. Thus, minimal disturbance was caused to the population as a result of sampling.

Two special trappings were conducted in February and May, 1976, to confirm that there were no significant differences in the numbers of crabs of each species trapped in the three sections of the study area within the same zone. On each occasion, a total of 30 baited traps were placed within Zone II. Ten traps were placed in each of the three sections, A, B and C. These traps were also left overnight, as described above, and the crabs were collected on the following day.

Results

(i) Losses of traps

There were some losses of data from traps during the study. When this occurred, the mean number of crabs per trap in a particular zone had to be calculated from fewer than 10 traps. Data were lost for the reasons discussed below.

(a) Although every effort was made to secure the traps in the mud, some were dislodged from their positions by water

movement as the tide changed. Some of these traps were found protruding from the surface of the mud and were thus inaccessible to crabs. Others had been completely removed from their holes and were found caught amongst the mangrove trees towards the back of the swamp. The results of 2% of traps set throughout the study (12 from a total of 640) were lost because of this.

(b) A further 2% of traps were discarded because the baits disappeared. The results of these traps were thus not directly comparable with the intact ones. Holes and small tooth marks were present in the tops of some of these traps. Small mammals, possibly bush rats, were probably responsible for the removal of these baits. In October, 1975, the baits had been removed from all 10 of the traps in Zone IV. The lids were intact on most of these traps and only two had holes or tooth marks in them. Baits were lost more often from traps towards the landward fringe of the swamp, which supported the suggestion that the baits were removed by small mammals.

(c) The results of 0.8% of traps (5 traps) had to be discarded because these traps partially filled with mud as the tide rose. The baits were buried under the mud and were no longer effective to attract crabs. This only happened in Zone I where the mud was very moist and of loose consistency.

In each of these cases the numbers of crabs were available from only 7, 8 or 9 traps in a zone. The mean number of crabs per trap from the remaining traps in that zone was substituted for the missing readings for purposes of analysis. On only one occasion, namely October 1975, were fewer than 7 intact traps available in any zone. Because the baits were missing

TABLE 3-4

Comparison of results of trapping from the three sections of the study area.

A. Mean numbers of crabs per trap in the three sections of Zone II during February and May, 1976.

Section	A	B	C
Sesarma erythrodactyla			
February	5.9	6.5	7.1
May	1.6	1.1	1.1
Paragrapsus laevis			
February	1.7	3.0	1.3
May	4.2	5.4	3.5

B. Analysis of variance of data from Zone II during February and May, 1976.

	Source of variation	Sum of Squares	Degrees of freedom	Mean Square	F-ratio
S. erythrodactyla					
February	Between Sections	7.20	2	13.60	0.28 n.s.
	Within Sections	348.30	27	12.90	
	Total	355.50	29		
May	Between Sections	1.67	2	0.83	0.59 n.s.
	Within Sections	38.20	27	1.41	
	Total	39.87	29		
P. laevis					
February	Between Sections	15.80	2	7.90	1.61 n.s.
	Within Sections	132.20	27	4.90	
	Total	148.00	29		
May	Between Sections	18.47	2	9.23	1.57 n.s.
	Within Sections	158.50	27	5.87	
	Total	176.97	29		

from all 10 traps in Zone IV, the results from this month were omitted from the analysis of the data.

(ii) Comparison between sections of the study area.

The data from the special trappings in February and May, 1976, were analysed by single factor analysis of variance. In the zone sampled, there were no significant differences in the numbers of Sesarma erythrodactyla or Paragrapsus laevis per trap in the three sections A, B and C. (Table 3-4). This confirmed the validity of sampling the three sections of the study area on successive occasions, rather than sampling at exactly the same sites each month.

(iii) Sesarma erythrodactyla

Analysis of variance was done on the pooled numbers of male and female S. erythrodactyla trapped throughout the study. There was, however, considerable heterogeneity of variances (Cochran's test: $P < 0.01$). This was not decreased by standard transformations of the data, to logarithms or square-roots, nor by omission of the extraordinarily high numbers of crabs trapped in December 1974 (Fig. 3-4). There was no obvious pattern of relationship between the mean number of crabs per trap and the between-traps variance in the four zones, nor between months (Fig. 3-4).

Because of this heterogeneity of variances, and because of the great power of the two-factor analysis of variance used, with 468 degrees of freedom in the Residual Mean Square (Table 3-5), it was concluded that the significant interaction found between

FIG. 3-4

Results of trapping Sesarma erythrodactyla (numbers of male and female crabs pooled). Mean numbers of crabs per trap (± 95% confidence limits) and multiple regression curves (broken lines) are shown. See text, pages 50 - 53 , for details.

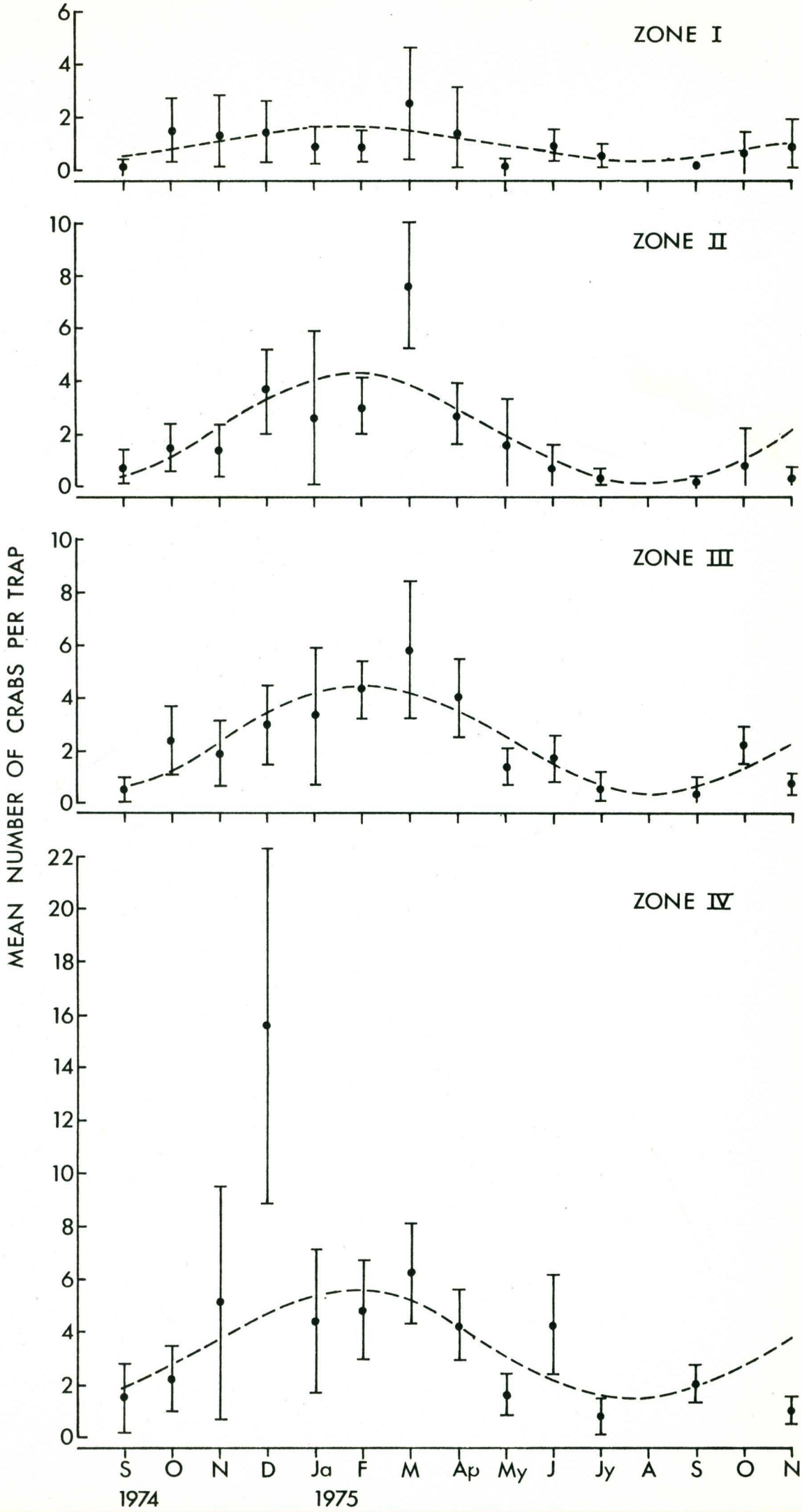

ZONE I
ZONE II
ZONE III
ZONE IV
MEAN NUMBER OF CRABS PER TRAP
0
2
4
6
8
10
12
14
16
18
20
22
S
O
N
D
Ja
F
M
Ap
My
J
Jy
A
S
O
N
1974
1975

TABLE 3-5

Analysis of variance of numbers of *Sesarma erythrodactyla* caught in traps.

Source of variation	Sum of squares	Degrees of freedom	Mean square	F-ratio
Between Zones	690.39	3	230.13	41.53**
Between Times of Sampling	1500.41	12	125.03	22.56**
Interaction: Zones x Times	1191.51	36	33.10	5.97**
Residual	2593.47	468	5.54	
Total	5975.79	519		

Cochran's test : $P < 0.01$

TABLE 3-6

Comparison of mean number of *Sesarma erythrodactyla* per trap in the four zones.

A. Rank order of mean number of crabs per trap for each zone (ranked from least to greatest).

	1974				1975								
Time of Sampling	S	O	N	D	Ja	F	M	Ap	My	J	Jy	S	N
Zone I	1	1	1	1	1	1	1	1	1	2	2	1	3
Zone II	3	2	2	3	2	2	4	2	3	1	1	2	1
Zone III	2	4	3	2	3	3	2	3	2	3	3	3	2
Zone IV	4	3	4	4	4	4	3	4	4	4	4	4	4

B. Mean number of crabs per trap in each zone, pooled over all samples.

Zone I	Zone II	Zone III	Zone IV
0.95	1.95	2.30	4.14

Zones and Times of sampling was a statistical artefact. The Interaction Mean Square was relatively small compared with the Residual Mean Square in the analysis of untransformed data (Table 3-5). The size of the F-ratio for Interaction was very small when compared with those of the highly significant main effects of Zones and Times of sampling. Thus, there were significant differences in mean numbers of crabs between the zones and from one time of year to another.

On the basis of this preliminary analysis, several further analyses were done to identify differences between Zones and Times of sampling in relation to the number of crabs trapped.

(a) Variation between Zones.

Significant differences between zones were found by a Kruskal-Wallis test (Hollander and Wolfe, 1973) of the rank-order of mean abundance of crabs, using each month's data as replicates of ranks for each zone. The rank-order and mean number of crabs per trap, pooled over all months, for each zone are shown in Table 3-6.

The Kruskal-Wallis multiple comparison of ranks (Hollander and Wolfe, 1973) demonstrated that the mean number of crabs per trap was significantly greater in Zone IV and decreased uniformly and significantly to be least in Zone I (as indicated in Table 3-6 and Fig. 3-4).

(b) Variation between Times of sampling

The mean numbers of crabs per trap in each of the zones were used as four replicates for each month in a single factor analysis of variance to test for differences

TABLE 3-7

Analysis of variance of mean numbers of *Sesarma erythrodactyla* per trap between Times of sampling.
(Mean numbers of crabs in each zone used as replicates for each month. Number in Zone IV in December, 1974, replaced by mean of numbers in November, 1974, and January, 1975).

Source of variation	Sum of squares	Degrees of freedom	Mean square	F-ratio
Between Months	99.48	12	8.29	4.84**
Within Months	66.83	39	1.71	
Total	166.31	51		

S.N.K. test: Mean in March, 1975, was only mean to differ significantly at P = 0.05.

between Times of sampling. The extraordinarily high reading in Zone IV for December, 1974, was replaced by the mean of the readings for November, 1974, and January, 1975, to reduce the heterogeneity of variances. There was a significant difference between months (Table 3-7). A Student-Neuman-Keul's multiple comparison of the mean in each month showed that only one month, March 1975, was significantly different from the others. This was partly a result of the high variability in the data.

The seasonal trends in numbers of crabs trapped were more usefully examined by regression analysis. Seasonal trends might be expected to approximate curvilinear models (e.g. Underwood, 1975). Since on inspection the abundance of crabs in each zone appeared to approximate sine curves, a multiple regression analysis was conducted to fit the results to the curve

$y = a + b_1 \sin X + b_2 \cos x$ in which

y = mean number of crabs per trap in a zone,

x = the month expressed as an angle between 0^o and 360^o,

a = intercept, and

b_1 and b_2 = regression coefficients.

a, b_1 and b_2 were estimated by multiple regression on sin x and cos x. The results are shown in Fig. 3-4. The multiple regressions for Zones II, III and IV were all significant (Table 3-8). Thus, the numbers of S. erythrodactyla increased in all three zones towards the warmer months of December to April and decreased towards the colder months of July to September. In Zone I the regression, although similar in shape, was not significantly different from a straight line. In Zone I, however,

TABLE 3-8

Analyses of variance of multiple regressions of results of trapping Sesarma erythrodactyla.

(Number in Zone IV in December, 1974, replaced by mean of numbers in November, 1974, and January, 1975)

Source of variation	Sum of squares	Degrees of freedom	Mean square	F-ratio
Zone I				
Regression on sin x + cos x	2.02	2	1.01	2.47 n.s.
Deviations from regression	3.69	9	0.41	
Total	5.71	11		
Zone II				
Regression on sin x + cos x	25.29	2	12.64	5.53*
Deviations from regression	20.56	9	2.28	
Total	45.85	11		
Zone III				
Regression on sin x + cos x	25.52	2	12.76	18.46**
Deviations from regression	6.22	9	0.69	
Total	31.74	11		
Zone IV				
Regression on sin x + cos x	22.56	2	11.28	8.32**
Deviations from regression	12.19	9	1.36	
Total	34.75	11		

there were very few crabs, compared with the other zones (Table 3-6).

The pooled numbers of male and female S. erythrodactyla rose uniformly in Zones II, III and IV during January and February, 1975, to reach a maximum in March, 1975, (Fig. 3-4). In the same period the numbers of female S. erythrodactyla in Zone II also rose to a maximum (Fig. 3-5). In contrast, the numbers of female S. erythrodactyla in Zones III and IV decreased slightly, but uniformly, during January, February and March, 1975 (Fig. 3-5). This decrease in the numbers of female crabs in Zones III and IV, at a time when total numbers of crabs were increasing to a maximum, and the corresponding increase in the numbers of female crabs in Zone II, provide some evidence of possible movement of female crabs from Zones III and IV into Zone II. In April, 1975, the numbers of female S. erythrodactyla decreased sharply in Zone II and increased in Zones III and IV. The movement of female S. erythrodactyla from Zone II back into Zones III and IV is considered possible.

No separate analyses of the numbers of male and female S. erythrodactyla could be conducted because of the relatively small numbers sampled. At no other times of the year were there any obvious variations in the seasonal trends in the numbers of either female or male S. erythrodactyla from the patterns shown by the total population (Fig. 3-4).

(c) Size frequency distribution

The size frequency distributions of S. erythrodactyla trapped in each zone over all months sampled are shown

FIG. 3-5

Results of trapping female Sesarma erythrodactyla. Mean numbers of crabs per trap (± 95% confidence limits) are shown.

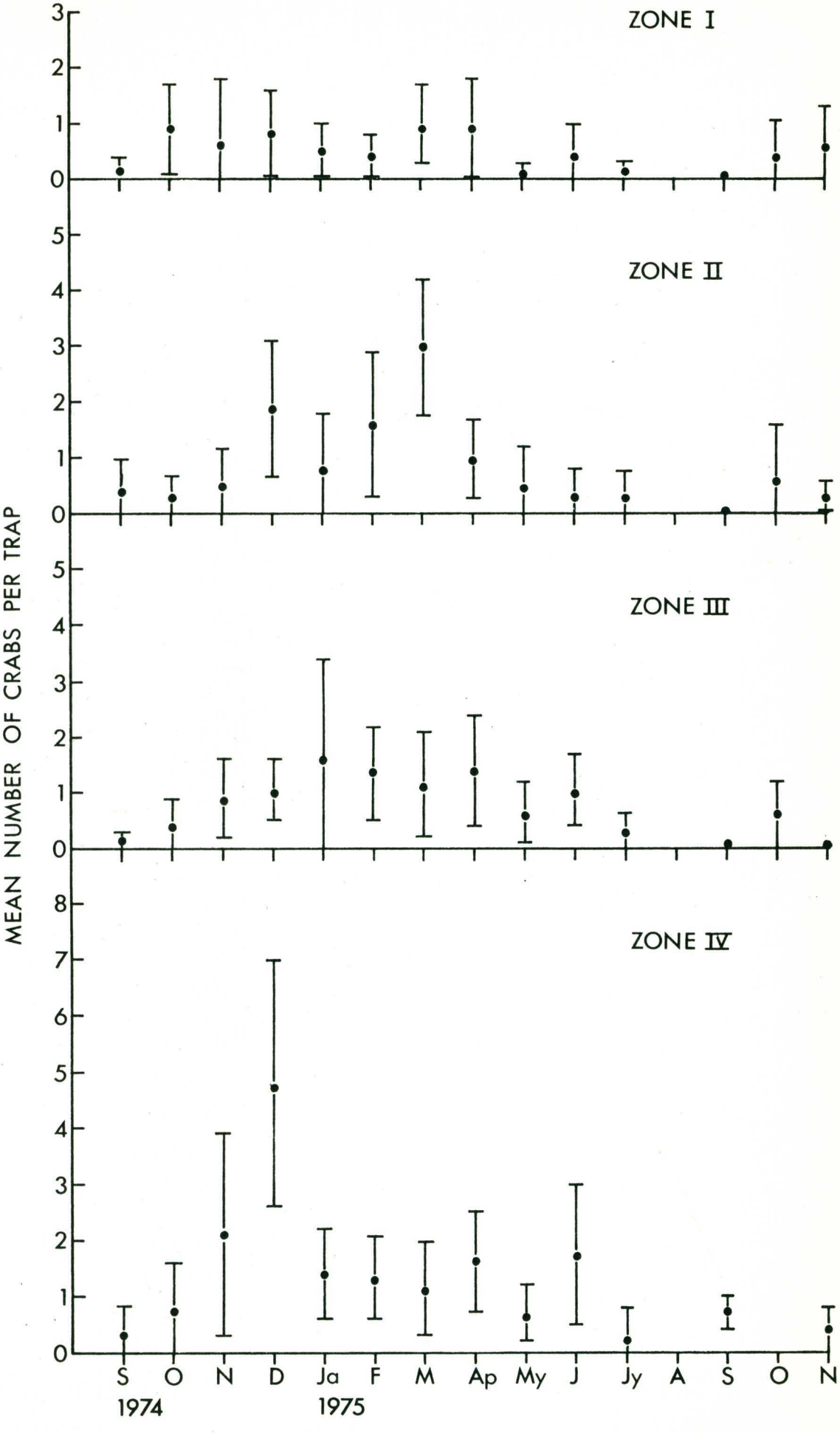

ZONE I
ZONE II
ZONE III
ZONE IV
MEAN NUMBER OF CRABS PER TRAP
S O N D Ja F M Ap My J Jy A S O N
1974
1975

TABLE 3-9

Comparison of numbers of male and female Sesarma erythrodactyla caught in traps in each zone

	Number of males	Number of females	Ratio: males/female	χ^2
Zone I	61	57	1.07	.14 n.s.
Zone II	143	105	1.36	5.82*
Zone III	189	96	1.97	30.35**
Zone IV	342	157	2.18	65.59**
Total	735	415	1.77	89.04**

TABLE 3-10

Comparison of numbers of gravid Sesarma erythrodactyla caught in traps in each zone.

	Number of gravid S. erythrodactyla caught	Percentage of total number of all gravid S. erythrodactyla caught in all zones.
Zone I	13	21
Zone II	30	48
Zone III	7	11
Zone IV	13	20
Total	63	

in Fig. 3-6. The size structures of the populations in Zones II, III and IV were very similar. The size class which occurred with greatest frequency had a carapace width of 15-20 mm. Higher percentages of smaller crabs and lower percentages of larger crabs were trapped in Zone I. The majority of crabs trapped in Zone I had a carapace width of 10-15 mm.

(d) Sex ratio

Significantly more male S. erythrodactyla were caught in traps than females ($\chi^2 = 89.04$; $P < 0.01$). The ratio of males to females over all zones was 1.77:1.

The observed sex ratio varied between zones. It rose uniformly from a minimum of 1.07 in Zone I to a maximum of 2.18 in Zone IV (Table 3-9).

(e) Occurrence of gravid Sesarma erythrodactyla

The percentage of gravid female S. erythrodactyla caught in traps in each zone during each month is shown in Fig. 3-7. Gravid females were found only from November to April. This corresponded to the time when the greatest total numbers of S. erythrodactyla were caught (Fig. 3-4) and also to the warmest months of the year. In Zones III and IV gravid female crabs were caught only in the more restricted period from January to March, 1975.

Of all gravid S. erythrodactyla caught in traps, 48% were caught in Zone II and a cumulative total of 69% were caught in Zones I and II (Table 3-10).

FIG. 3-6

Size-frequency distributions of Sesarma erythrodactyla caught in traps in each zone over all months sampled.

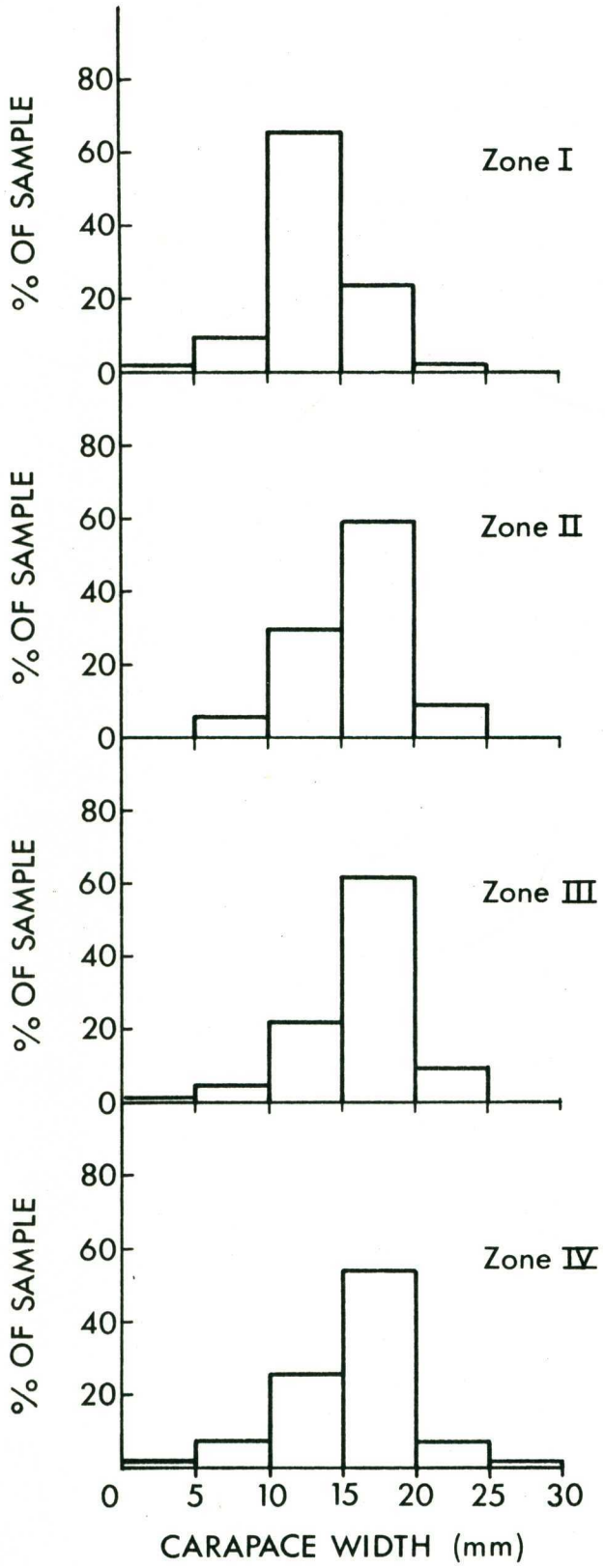

% OF SAMPLE
80
60
40
20
0
Zone I
Zone II
Zone III
Zone IV
0
5
10
15
20
25
30
CARAPACE WIDTH (mm)

FIG. 3-7

Percentages of gravid Sesarma erythrodactyla caught in traps in each zone during each month. Numbers above points on graphs show total numbers of female S. erythrodactyla caught in traps during each month.

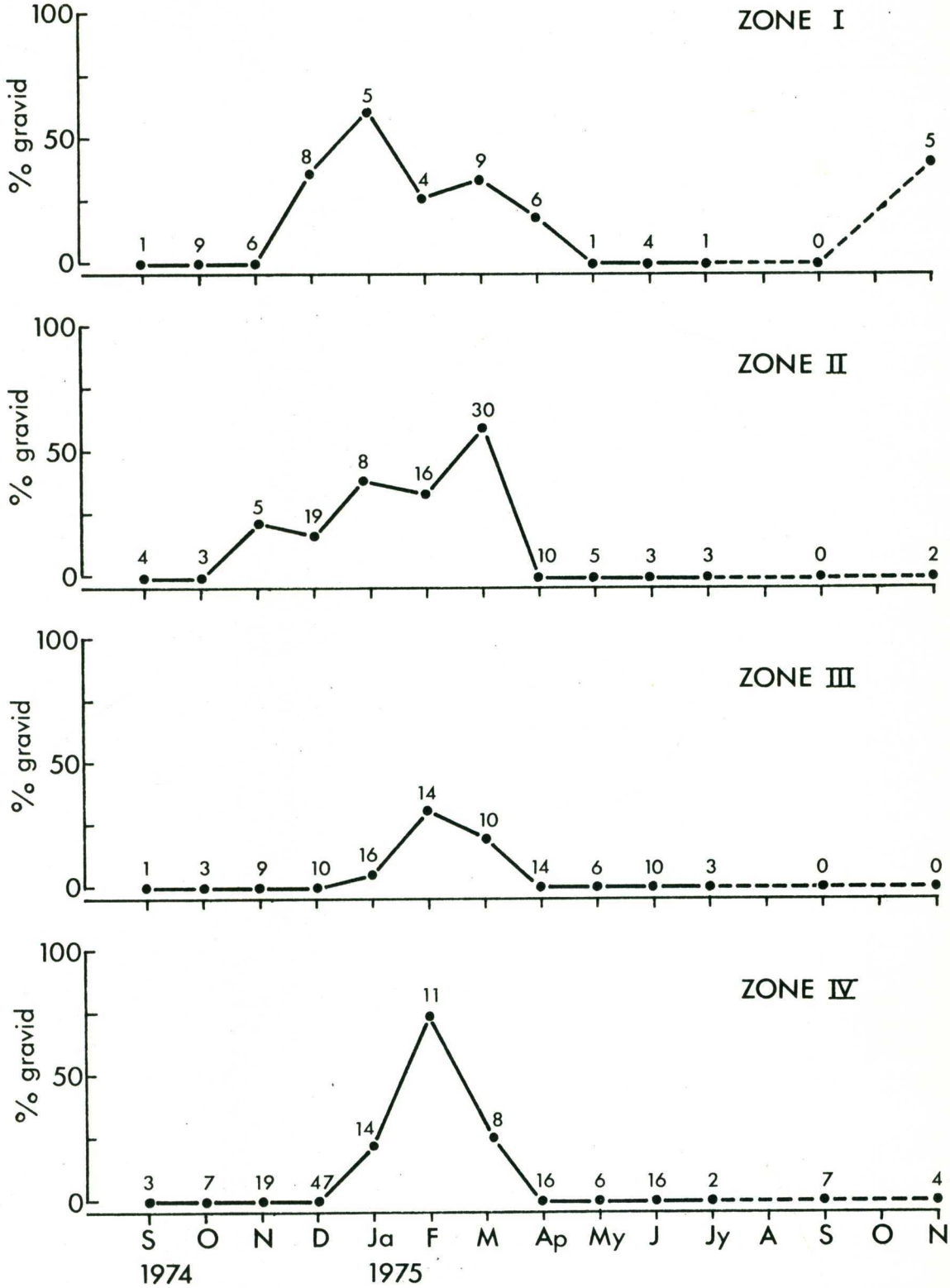

ZONE I
% gravid
100
50
0
1 9 6 8 5 4 9 6 1 4 1 0 5
ZONE II
% gravid
100
50
0
4 3 5 19 8 16 30 10 5 3 3 0 2
ZONE III
% gravid
100
50
0
1 3 9 10 16 14 10 14 6 10 3 0 0
ZONE IV
% gravid
100
50
0
3 7 19 47 14 11 8 16 6 16 2 7 4
S O N D Ja F M Ap My J Jy A S O N
1974
1975

TABLE 3-11

Analysis of variance of numbers of *Paragrapsus laevis* caught in traps

Source of variation	Sum of squares	Degrees of freedom	Mean square	F-ratio
Between Zones	810.29	3	270.10	56.78**
Between Times of sampling	535.42	12	44.62	9.38**
Interaction: Zones x Times	991.60	36	27.54	5.79**
Residual	2226.41	468	4.76	
Total	4563.72	519		

Cochran's test: $P < 0.01$

TABLE 3-12

Comparison of the mean numbers of *Paragrapsus laevis* in the four zones.

A. Rank order of mean number of crabs per trap for each zone (ranked from least to greatest).

Time of Sampling	1974				1975								
	S	O	N	D	Ja	F	M	Ap	My	J	Jy	S	N
Zone I	4	3	4	4	2	1	2	2	3	3	2	2	1
Zone II	3	4	1	3	4	4	4	4	4	4	3	4	4
Zone III	2	2	2	2	1	3	3	3	2	2	4	3	2
Zone IV	1	1	3	1	3	2	1	1	1	1	1	1	3

B. Mean number of crabs per trap in each zone, pooled over all samples

Zone I	Zone II	Zone III	Zone IV
2.97	4.49	2.15	1.07

(iv) Paragrapsus laevis

As with the data for S. erythrodactyla, a preliminary two-factor analysis of variance of the pooled numbers of male and female P. laevis indicated significant differences between Zones and Times of sampling (Table 3-11). There was, however, significant heterogeneity of between-trap variances (Cochran's test: $P < 0.01$) which could not be stabilised by standard logarithmic or square-root transformations of the data. There was no obvious relationship between the mean number of crabs per trap and the between-traps variance in the four zones (Fig. 3-8). Again there was a significant interaction between Zones and Times of sampling. This accounted for a relatively small proportion of the total variance, compared with the main effects of Zones and Times of sampling (Table 3-11). As with S. erythrodactyla, it was assumed that the significant interaction was due to the heterogeneity of variances and the great sensitivity of the analysis due to the large number of degrees of freedom in the Residual Mean Square. Thus, the analysis gave some indication of significant differences in the mean number of P. laevis between the zones and from one time of year to another. These differences were further investigated by the analyses described below.

(a) Variation between Zones

Significant differences between zones were found by a Kruskal-Wallis test of the rank-order of mean abundance of crabs, using each month's data as replicates of ranks for each zone. The rank-orders and mean numbers of crabs per trap, pooled over all months, for each zone are shown in Table 3-12.

FIG. 3-8

Results of trapping Paragrapsus laevis (numbers of male and female crabs pooled). Mean numbers of crabs per trap (± 95% confidence limits) and multiple regression curves (broken lines) are shown. See text, pages 55 - 58 , for details.

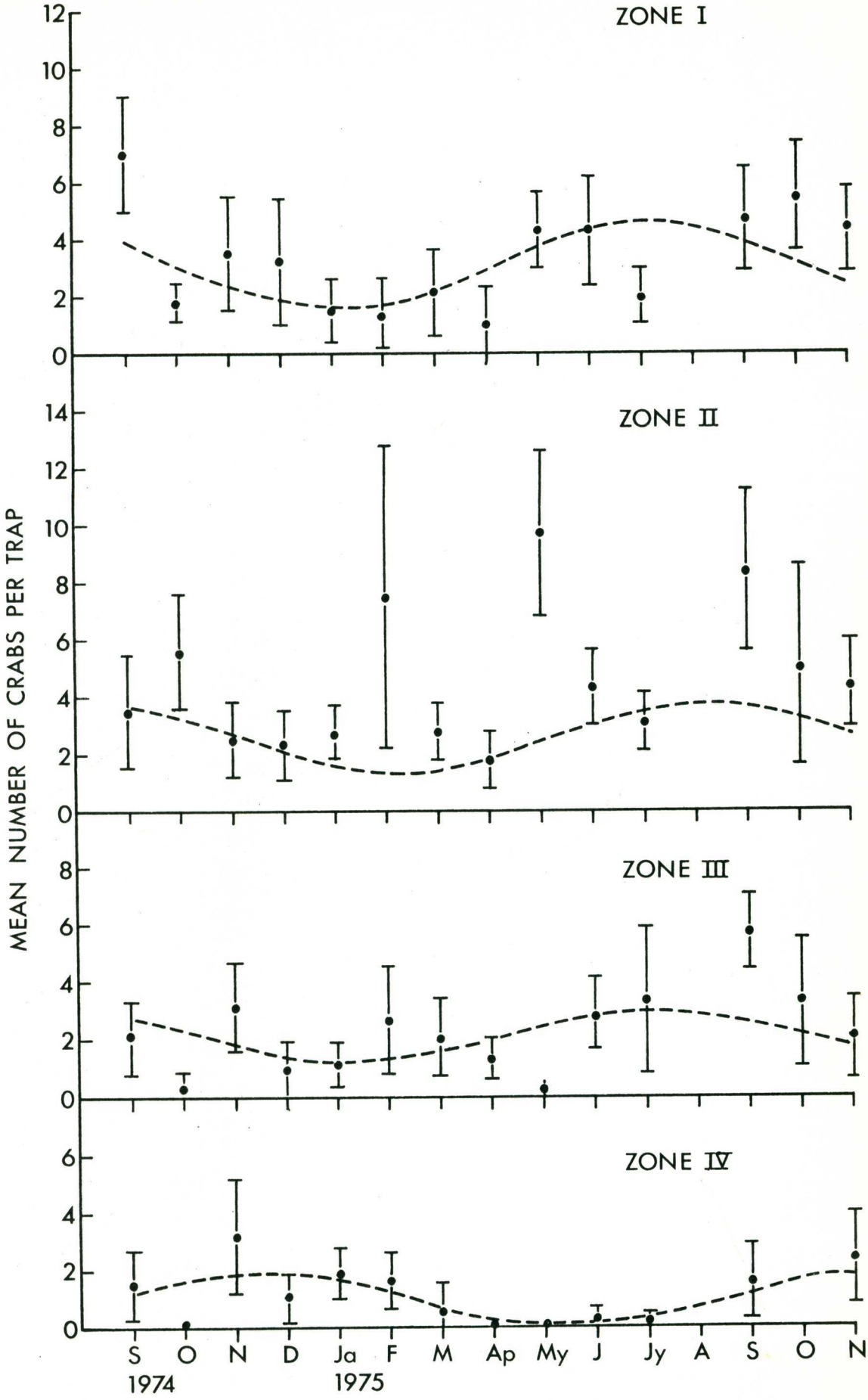

ZONE I
ZONE II
ZONE III
ZONE IV
MEAN NUMBER OF CRABS PER TRAP
0
2
4
6
8
10
12
14
S O N D Ja F M Ap My J Jy A S O N
1974
1975

TABLE 3-13

Analyses of variance of mean numbers of Paragrapsus laevis per trap between Times of sampling. (Mean numbers of crabs in each zone used as replicates for each month)

Source of variation	Sum of squares	Degrees of freedom	Mean square	F-ratio
A. Analysis over 13 months and 4 zones.				
Between Months	56.35	12	4.70	1.09 n.s.
Within Months	167.88	39	4.3	
Total	224.23	51		
B. Analysis over 12 months (omit May, 1975) and 4 zones.				
Between Months	54.76	11	4.98	1.67 n.s.
Within Months	107.61	36	2.99	
Total	162.37	47		
C. Analysis over 13 months and 3 zones (omit Zone II)				
Between Months	36.61	12	3.05	1.28 n.s.
Within Months	62.10	26	2.39	
Total	98.71	38		

The Kruskal-Wallis multiple comparison of ranks demonstrated that the mean number of crabs per trap was significantly greater in Zone II and decreased significantly among the other three zones in the order Zone I, Zone III and Zone IV (as indicated in Table 3-12 and Fig. 3-8).

(b) Variation between Times of sampling

A single factor analysis of variance using the mean number of P. laevis per trap for each of the four zones as replicates for each time of sampling showed no significant differences between months (Fig. 3-8, Table 3-13A). It was considered that the non-significance of this analysis might be due to the very large variance for the ninth month (May, 1975) and the analysis was repeated with this month omitted. This analysis was also non-significant. (Table 3-13B). A third attempt at this analysis, omitting the very variable results of Zone II and thus with only three replicates for the mean number of crabs for each month, also showed no significant differences between the months in the mean numbers of crabs sampled (Table 3-13C).

As with S. erythrodactyla the seasonal trends in numbers of crabs were more usefully examined by regression analysis. A multiple regression analysis was used to fit the results to the curve $y = a+b_1 \sin x + b_2 \cos x$ in which

y = mean number of crabs per trap in a zone,

x = the month expressed as an angle between 0^o and 360^o,

a = intercept, and

b_1 and b_2 = regression coefficients.

a, b_1 and b_2 were estimated by multiple regression on sin x and cos x. The regressions on sin x + cos x for all four zones

TABLE 3-14

Analyses of variance of multiple regressions of results of trapping *Paragrapsus laevis*.

Source of variation	Sum of squares	Degrees of freedom	Mean square	F-ratio
Zone I				
Regression on sin x + cos x	13.66	2	6.83	2.91 n.s.
Deviations from regression	21.14	9	2.35	
Total	34.80	11		
Zone II				
Regression on sin x + cos x	5.89	2	2.94	0.37 n.s.
Deviations from regression	71.71	9	7.97	
Total	77.60	11		
Zone III				
Regression on sin x + cos x	4.13	2	2.07	0.83 n.s.
Deviations from regression	22.39	9	2.49	
Total	26.52	11		
Zone IV				
Regression on sin x + cos x	4.81	2	2.40	3.58 n.s.
Deviations from regression	6.04	9	0.67	
Total	10.85	11		
Zone I and Zone III pooled				
Regression on sin x + cos x	16.28	2	8.14	3.49*
Deviations from regression	49.73	21	2.37	
Total	66.01	23		

were non-significant (Table 3-14).

Inspection of the data (Fig. 3-8) indicated that Zones I and III possibly followed a cosine curve. This was supported by the fact that while in the previous analysis neither zone was significant on cos x + sin x, Zone I was significant on cos x. Furthermore, when the results of Zones I and III were pooled and a regression used on sin x + cos x, it was significant (Table 3-14). The multiple regressions on sin x + cos x for Zones I and III are shown in Fig. 3-8.

Zone II was omitted from the above analysis because of the very much greater variability there. However, a multiple regression line drawn from the pooled results of zones I and III, fits the data in Zone II quite well (Fig. 3-8).

Zone IV contained the smallest numbers of P. laevis and on inspection variation in the numbers of P. laevis there appeared to follow a sine curve (Fig. 3-8). As well, while the original regression analysis for this zone on sin x + cos x was non-significant, it was significant on sin x alone (Table 3-14). The regression on sin x + cos x for Zone IV is shown in Fig. 3-8.

The analysis of variance discussed on page 55 is considerably more powerful than the rank-order and regression analyses used here. Thus, although no significant difference among times of sampling could be determined reliably on sin x + cos x, the original analysis of variance indicatedthat there are some trends which match those found by regression analysis using only cos x for Zones I and III and sin x for Zone IV. This contrasts with the situation in S. erythrodactyla where varia-

bility among Zones and Times of sampling was more consistent. To interpret fully the seasonal patterns of change of abundance of P. laevis will involve investigation of the sources of heterogeneity of variance and more intensive sampling than was possible in the present investigation.

No separate analyses of the numbers of male and female P. laevis were conducted because of the relatively small numbers sampled. At no time of the year was there any obvious variation in the seasonal trends in the numbers of either male or female P. laevis from the patterns shown by the total population (Fig. 3-8).

(c) Size frequency distribution

The size frequency distributions of P. laevis trapped in each zone over all months sampled are shown in Fig. 3-9. The size structures of the populations of crabs in Zones I, II and III were fairly similar although there were greater percentages of crabs with carapace widths in the range 10-20 mm in Zone I. The majority of crabs collected in Zone IV had carapaces in the range 15-25 mm wide.

(d) Sex ratio

There was no significant difference between the numbers of male and female P. laevis trapped over all zones ($\chi^2 = 2.84$; $P > 0.05$).

Among individual zones, only Zone IV showed a significant difference between the numbers of male and female crabs. In Zone IV there were significantly more female than male crabs ($\chi^2 = 18.05$; $P < 0.01$). The observed ratio of males to females in this zone was 0.46:1.

FIG. 3-9

Size-frequency distributions of Paragrapsus laevis caught in traps in each zone over all months sampled.

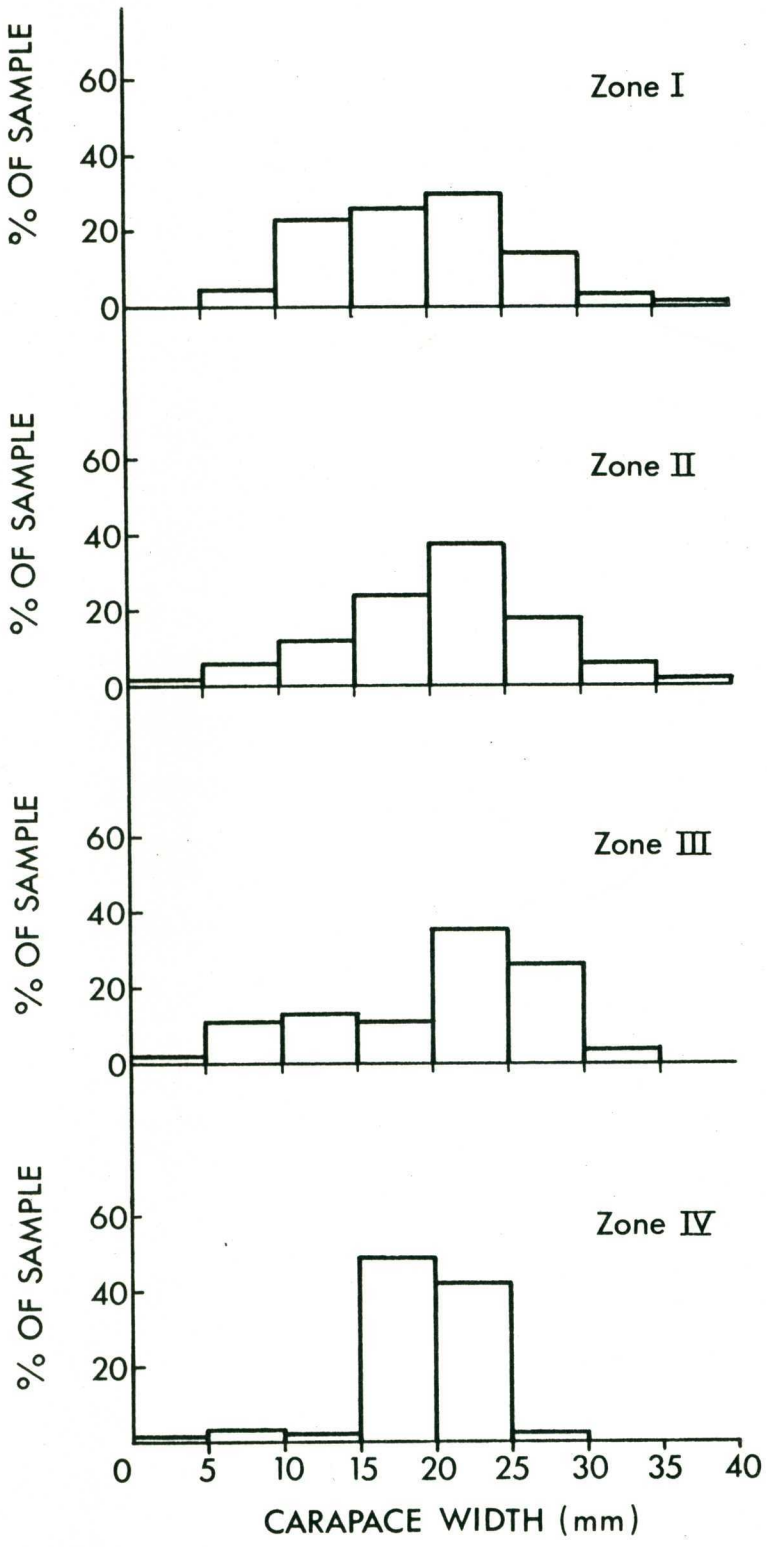

% OF SAMPLE
60
40
20
0
Zone I
% OF SAMPLE
60
40
20
0
Zone II
% OF SAMPLE
60
40
20
0
Zone III
% OF SAMPLE
60
40
20
Zone IV
0
5
10
15
20
25
30
35
40
CARAPACE WIDTH (mm)

TABLE 3-15

Comparison of numbers of gravid *Paragrapsus laevis* caught in traps in each zone, pooled over all samples.

	Number of gravid *P. laevis* caught	Percentage of total number of all gravid *P. laevis* caught in all zones
Zone I	42	82
Zone II	6	12
Zone III	2	4
Zone IV	1	2
Total	51	

TABLE 3-16

Comparison of the numbers of *Heloecius cordiformis* caught in traps in each zone, pooled over all samples.

	Number of crabs caught	Number of crabs caught per trap	Percentage of total number of all *H. cordiformis* caught in all zones
Zone I	60	0.46	69.0
Zone II	13	0.10	14.9
Zone III	8	0.06	9.2
Zone IV	6	0.05	6.9
Total	87	0.17	

(e) Occurrence of gravid Paragrapsus laevis

The percentage of gravid female P. laevis caught in traps in each zone during each month is shown in Fig. 3-10. Gravid P. laevis were only trapped from May to November, except for one crab caught in Zone IV in February, 1975.

Of all gravid P. laevis caught in traps, 82% were caught in Zone I and 12% in Zone II (Table 3-15). Of the remaining three crabs, two were caught in Zone III and one in Zone IV.

(v) Heloecius cordiformis

Eighty-seven H. cordiformis were caught in traps throughout the trapping programme. The majority of these crabs were caught in Zone I. The small numbers of crabs caught in the other three zones decreased uniformly from Zone II to Zone IV (Table 3-16). Greater numbers were caught during summer and autumn than during winter and spring (Fig. 3-11).

The carapace width of most H. cordiformis trapped was in the range of 10-20 mm; 60% had a carapace width between 15-20 mm (Fig. 3-12).

Significantly more male H. cordiformis were caught in traps than females ($\chi^2 = 19.32$; $P < 0.01$). The ratio of males to females was 2.8:1.

Only 5 gravid female H. cordiformis were caught in traps throughout the study. These were caught in Zone I in January, February, March and July, 1975 (Table 3-17).

FIG. 3-10

Percentages of gravid Paragrapsus laevis caught in traps in each zone during each month. Numbers above points on graphs show total numbers of female P. laevis caught in traps during each month.

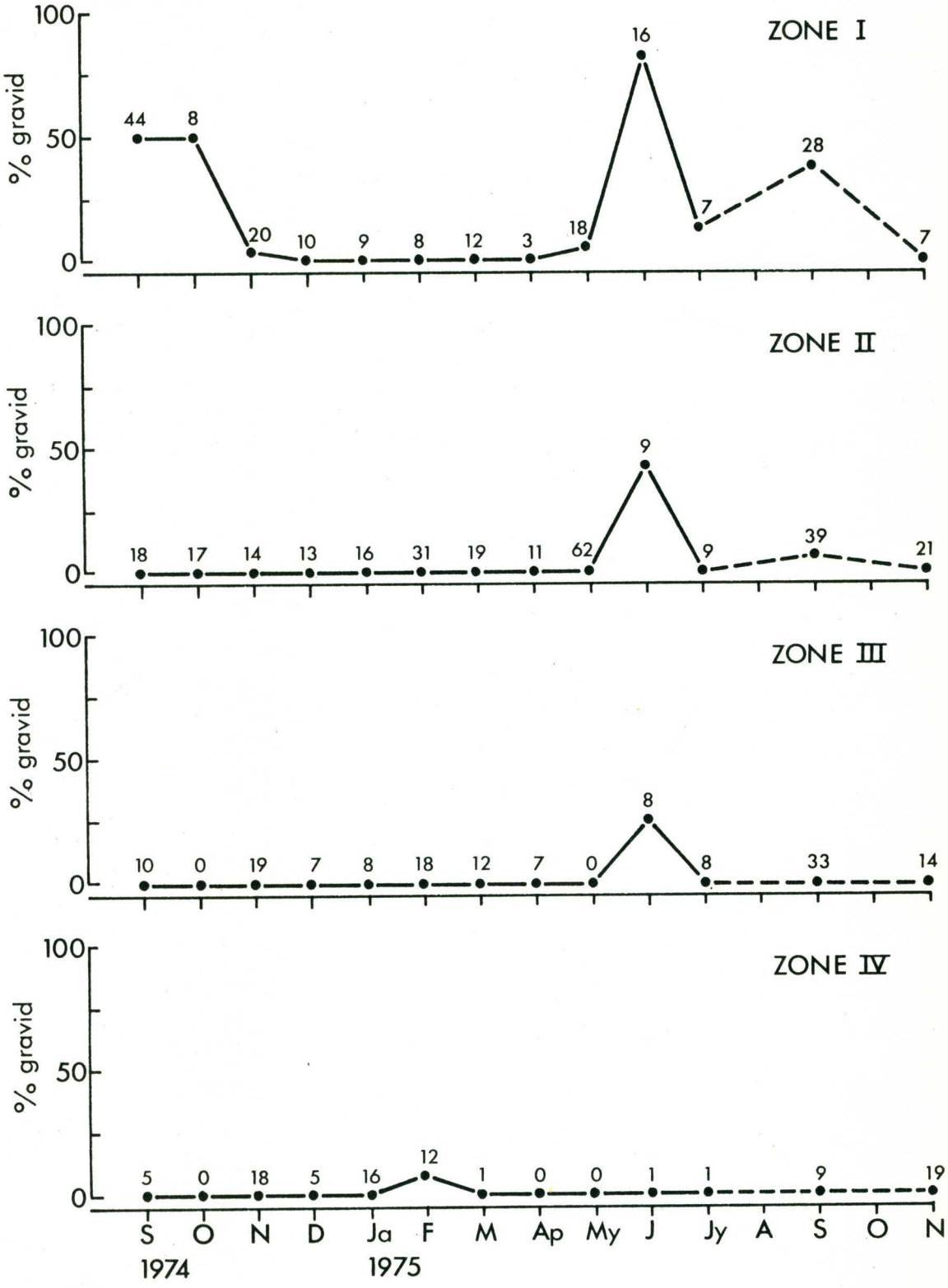

ZONE I
% gravid
100
50
0
44 8 20 10 9 8 12 3 18 16 7 28 7
ZONE II
% gravid
100
50
0
18 17 14 13 16 31 19 11 62 9 9 39 21
ZONE III
% gravid
100
50
0
10 0 19 7 8 18 12 7 0 8 8 33 14
ZONE IV
% gravid
100
50
0
5 0 18 5 16 12 1 0 0 1 1 9 19
S O N D Ja F M Ap My J Jy A S O N
1974
1975

FIG. 3-11

Results of trapping Heloecius cordiformis, Helograpsus haswellianus, Helice leachii and Ilyograpsus paludicola (numbers of male and female crabs pooled). Mean numbers of crabs caught per trap, pooled over all zones, are shown.

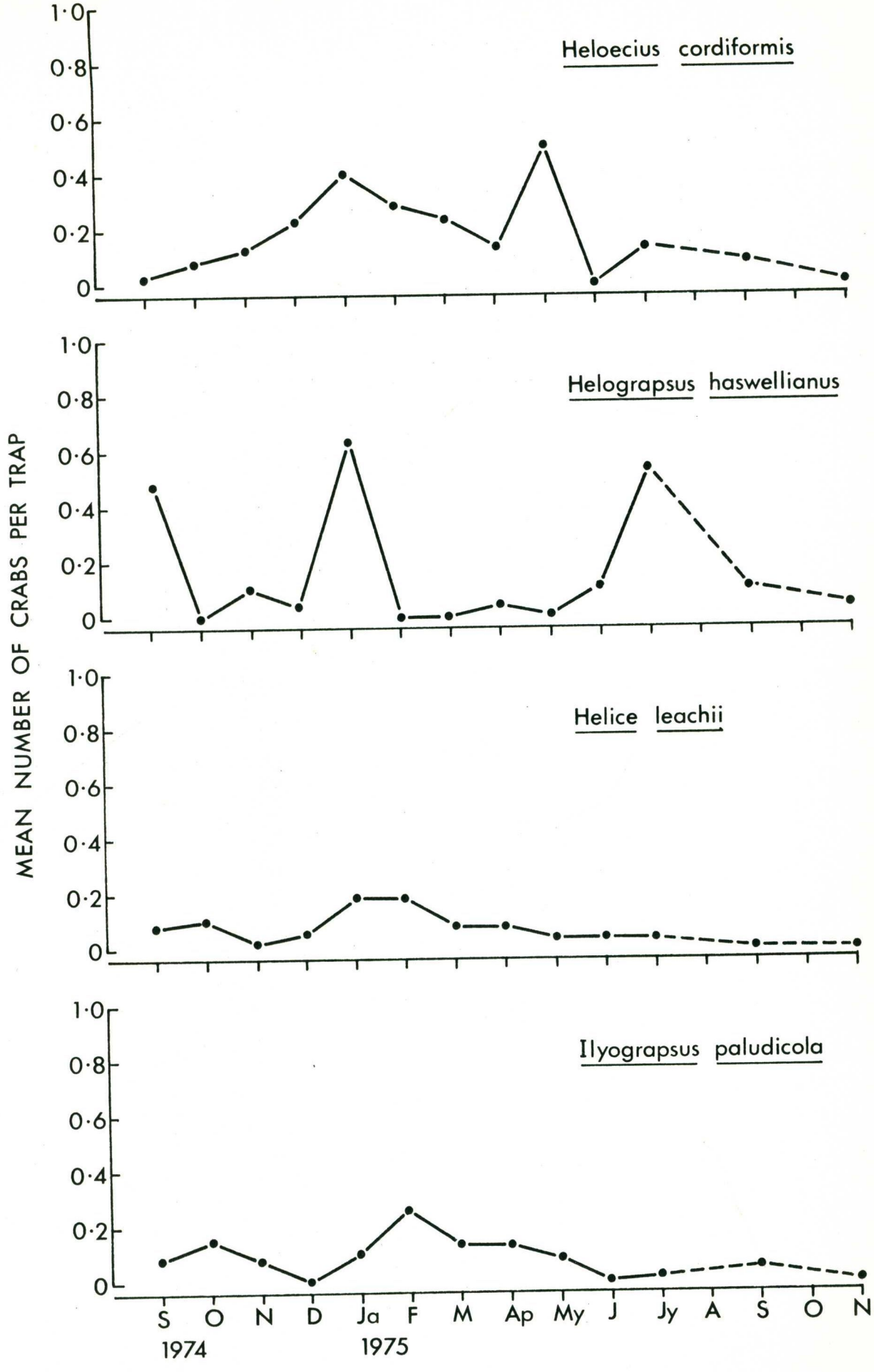

Heloecius cordiformis
Helograpsus haswellianus
Helice leachii
Ilyograpsus paludicola
MEAN NUMBER OF CRABS PER TRAP
1·0
0·8
0·6
0·4
0·2
0
S O N D Ja F M Ap My J Jy A S O N
1974
1975

FIG. 3-12

Size-frequency distributions of Heloecius cordiformis, Australoplax tridentata, Pilumnopeus serratifrons, Helograpsus haswellianus, Helice leachii and Ilyograpsus paludicola caught in traps (pooled over all zones and months).

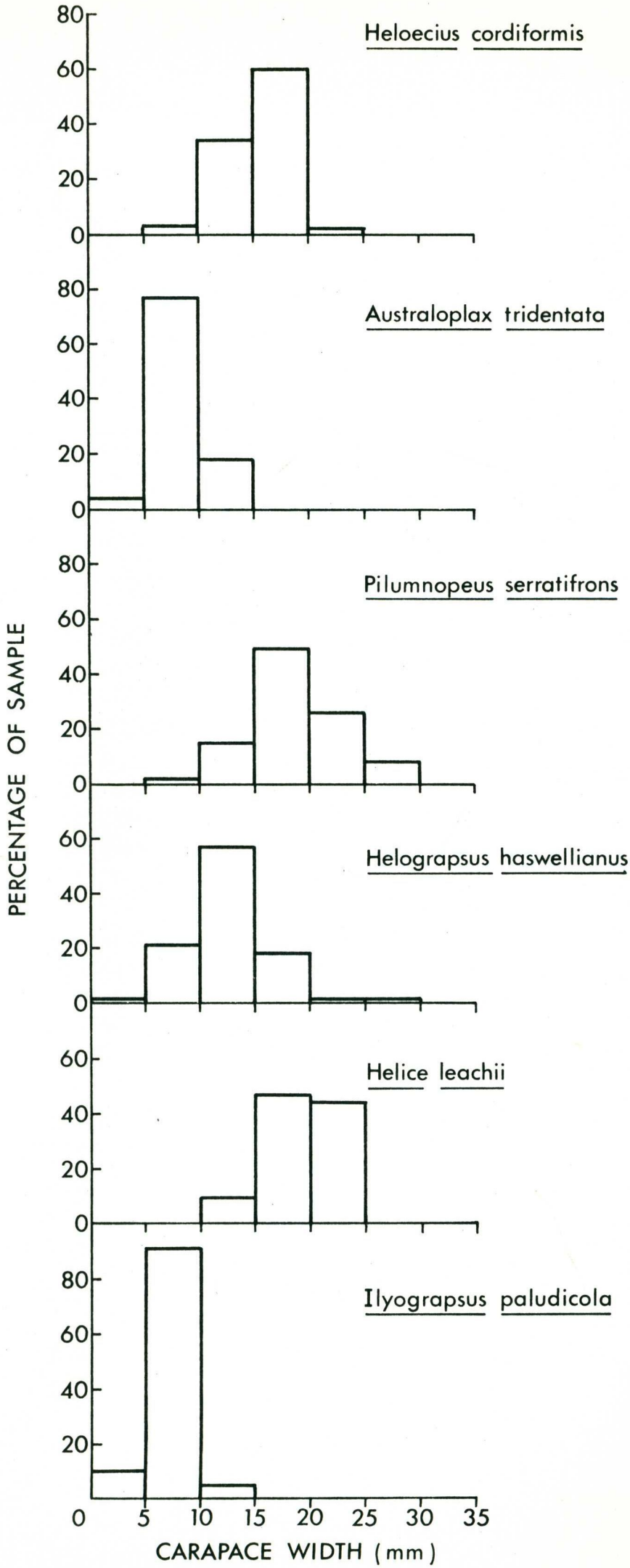

Heloecius cordiformis
Australoplax tridentata
Pilumnopeus serratifrons
Helograpsus haswellianus
Helice leachii
Ilyograpsus paludicola
PERCENTAGE OF SAMPLE
0
20
40
60
80
0
5
10
15
20
25
30
35
CARAPACE WIDTH (mm)

TABLE 3-17

Months in which gravid female crabs of five species were caught in traps during the study.

	1974				1975								
	S	O	N	D	Ja	F	M	Ap	My	J	Jy	S	N
Heloecius cordiformis	-	-	-	-	x	x	x	-	-	-	x	-	-
Australoplax tridentata	-	-	-	-	-	-	x	x	-	-	-	-	-
Pilumnopeus serratifrons	-	-	x	x	x	-	-	-	-	-	-	-	-
Helice leachii	-	-	-	-	-	x	-	-	-	-	-	-	-
Ilyograpsus paludicola	x	x	-	-	-	x	x	x	-	-	-	x	-

x, months in which gravid females were caught.

-, months in which no gravid females were caught.

TABLE 3-18

Analysis of variance of mean numbers of Pilumnopeus serratifrons per trap between Times of sampling (All data transformed to natural logarithms. Numbers of crabs per trap used as replicates for each month)

Source of variation	Sum of squares	Degrees of freedom	Mean square	F-ratio
Between Months	22.64	12	1.89	6.83**
Within Months	32.34	117	0.28	
Total	54.98	129		

Ja'75 D'74 N'74 F'75 M'75 Ap'75 N'75 J'74 S'74 Jy'74 My'74 O'74 S'74

(vi) Pilumnopeus serratifrons

All 145 P. serratifrons trapped throughout the trapping programme were caught in Zone I, except for one crab caught in Zone II. A single factor analysis of variance in which the mean numbers of crabs per trap were used as replicates for each month and in which all data were transformed to ln (x+1) to stabilise the variances indicated a significant difference among months. A Student-Neuman-Keul's multiple comparison of the means in each month showed that the greatest numbers of crabs were caught in December, 1974, and January, 1975 (Table 3-18; Fig. 3-13). The smallest numbers of crabs were caught in the colder months of May to September (Fig. 3-13).

The carapace width of P. serratifrons caught in traps ranged from 5-25 mm. Crabs with a carapace width of 15-20 mm occurred in greatest frequency (Fig. 3-12).

Significantly more male P. serratifrons were caught than females ($\chi^2 = 29.1$; $P < 0.01$). The observed ratio of males to females was 2.6:1.

Only 8 gravid female P. serratifrons were caught in traps throughout the study. These were all caught in summer (Table 3-17).

(vii) Australoplax tridentata

Twenty-two A. tridentata were trapped throughout the study. All were caught in Zone I, except for one crab caught in each of Zones II, III and IV. Too few A. tridentata were caught to enable any uniform seasonal changes in abundance to be detected.

FIG. 3-13

Results of trapping Pilumnopeus serratifrons (numbers of male and female crabs pooled). Mean numbers of crabs caught per trap, pooled over all zones, are shown. All data are transformed to ln (number + 1).

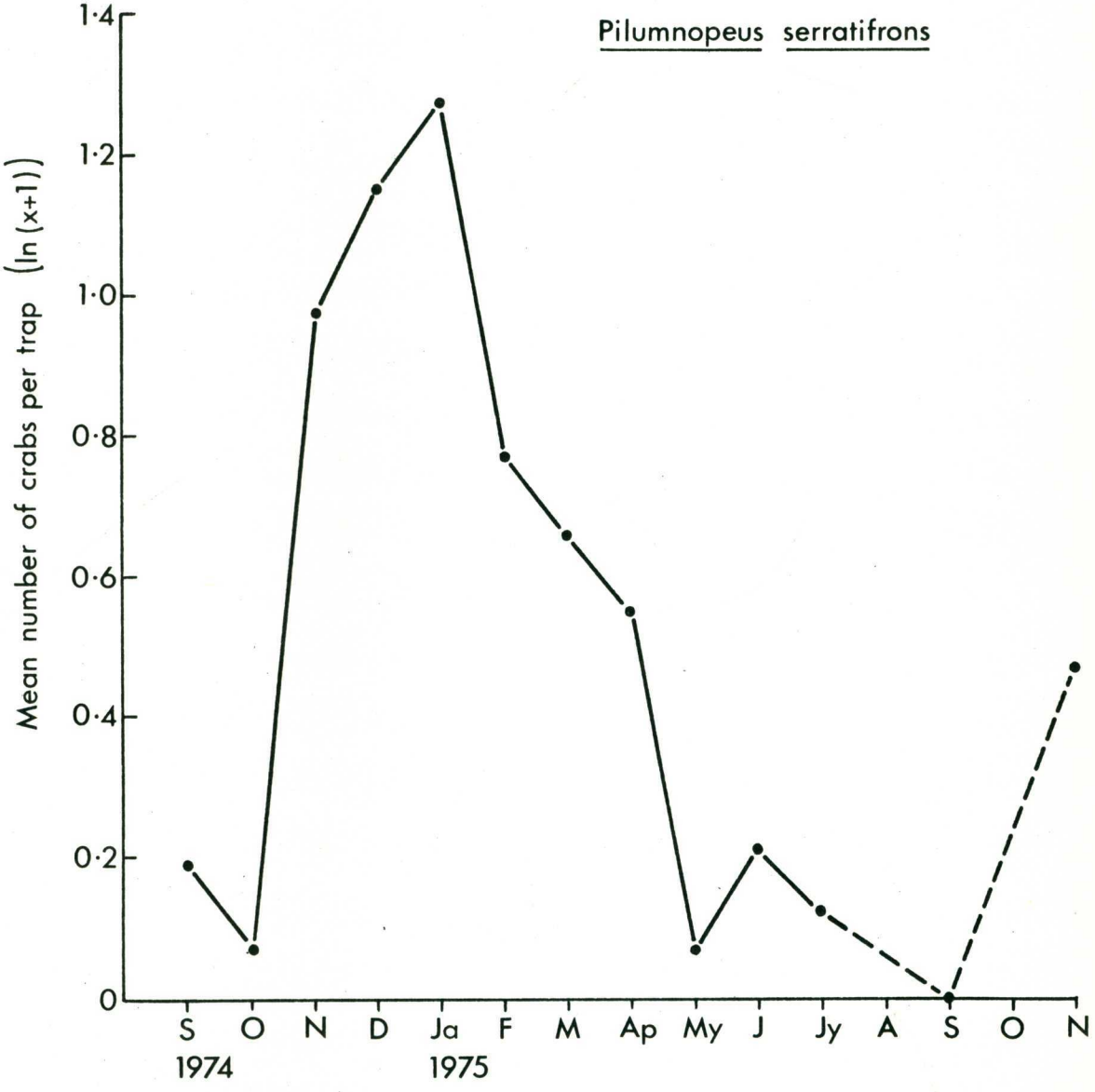

Pilumnopeus serratifrons
Mean number of crabs per trap (ln (x+1))
1·4
1·2
1·0
0·8
0·6
0·4
0·2
0
S O N D Ja F M Ap My J Jy A S O N
1974
1975

TABLE 3-19

Comparison of the numbers of Helice leachii caught in traps in each zone, pooled over all samples.

	Numbers of crabs caught	Mean number of crabs caught per trap	Percentage of total number of all H. leachii caught in all zones
Zone I	0	0	0
Zone II	4	0.03	12.5
Zone III	18	0.14	56.2
Zone IV	10	0.08	31.3
Total	32		

The carapace width of A. tridentata caught in traps ranged from 0-15 mm; 77% had a carapace width in the 5-10 mm range (Fig. 3-12).

There was no significant difference between the numbers of male and female A. tridentata ($\chi^2 = 0.73$; $P > 0.05$). The observed ratio of males to females was 1.44:1.

Only 3 gravid female A. tridentata were caught in traps throughout the study. These were caught in March and April, 1975 (Table 3-17).

(viii) Helograpsus haswellianus

Eighty H. haswellianus were trapped during the study. All were found in Zone IV. Because of the relatively small number of crabs caught and the patchiness in the times when they were caught, no consistent seasonal variation in numbers could be detected. (Fig. 3-11).

Carapace widths of H. haswellianus caught in traps ranged from 0-30 mm. The majority of crabs had carapace widths in the range 5-20 mm; 58% had a carapace width of 10-15 mm (Fig. 3-12).

There was no significant difference between the numbers of male and female H. haswellianus trapped. ($\chi^2 = 1.25$; $P > 0.05$).

No gravid female H. haswellianus were caught in traps throughout the study.

(ix) Helice leachii

Thirty-two H. leachii were caught in traps during the study. The majority were caught in Zones III and IV. (Table 3-19).

Greater numbers of crabs were caught during summer than during winter (Fig. 3-11).

Carapace widths of H. leachii ranged from 19-25 mm; the majority were in the 15-25 mm range (Fig. 3-12).

There was no significant difference between the numbers of male and female crabs caught ($\chi^2 = 1.13$; $P > 0.05$).

One gravid female H. leachii was caught in February, 1975 (Table 3-17).

(x) Ilyograpsus paludicola

Forty-one specimens of this small species of crab were caught in traps during the study. I. paludicola was restricted to Zone I, except for a single specimen caught in Zone II. Larger numbers of this species were caught during summer than during winter (Fig. 3-11).

The carapace width of I. paludicola caught ranged from 0-15 mm; 85% of crabs had a carapace width in the range 5-10 mm (Fig. 3-12).

There was no significant difference between the numbers of males and females caught ($\chi^2 = 1.2$; $P > 0.05$).

Nine gravid females were caught in traps during the study. These were caught in September and October, 1974, and February, March, April and September, 1975 (Table 3-17).

3.33 Photographic Census

Materials and Methods

Samples were taken monthly from November, 1974, to February, 1976, with exception of May and July, 1975, when field trips could not be made. Five randomly placed 0.25 m^2 quadrats were marked out on the ground with four 0.5 m lengths of dowel timber at low tide in each zone. A 35 mm single lens reflex camera with wide angle lens and flashlight was mounted on a tripod above a quadrat and focussed onto the marked area. This was then left for five minutes to allow re-emergence of crabs from their burrows following the disturbance caused by setting up the camera. The camera shutter was then opened and closed by an extension release from a distance of about six metres. This was repeated for each quadrat in turn. Preliminary trials showed that there were no differences in the numbers of crabs that re-emerged from their burrows whether the camera was left for 5, 10 or 15 minutes before the shutter was released. The shortest time of 5 minutes was therefore chosen.

The colour slides obtained were examined under a dissecting microscope at 20 X magnification and the numbers of crabs of each species counted. It was not possible to determine the sex nor to measure the carapace width of individuals, nor was it possible to identify gravid females accurately by this sampling method. In a few cases it was also not possible to identify the species of a crab, particularly when the crab was partially hidden beneath mangrove leaves, behind pneumatophores or inside the entrance to a burrow. These crabs were ignored.

TABLE 3-20

Comparison of numbers of Heloecius cordiformis sampled in Zones I, II and III in photographic census.

A. Analysis of variance of numbers of H. cordiformis sampled (all data transformed to natural logarithms).

Source of variation	Sum of squares	Degrees of freedom	Mean square	F-ratio
Between Zones	31.24	2	15.62	51.50**
Between Times of sampling	56.82	13	4.37	14.41**
Interaction: Zones x Times	12.41	26	0.48	1.57 n.s.
Residual	50.96	168	0.30	
Total	151.43	209		

B. Multiple comparison of mean numbers of H. cordiformis per 0.25 m^2 in each zone (pooled over all months sampled) and month (pooled over all zones).

Zone I	Zone II	Zone III
1.98	1.72	1.06

(S.N.K. test: All means significantly different, $P<0.05$)

A'75	J'75	F'76	D'75	S'75	N'75	F'75	Ap'75	D'74	O'74	Ja'75	N'74	M'75	Ja'76
0.32	0.71	1.27	1.46	1.55	1.61	1.71	1.78	1.81	1.82	1.83	1.89	1.99	2.5

(S.N.K. test: Means which were not significantly different, $P>0.05$, are underlined)

Results

The majority of crabs photographed by this sampling method were Heloecius cordiformis and the data collected on this species are discussed first, followed by those data collected on other species.

Heloecius cordiformis

The mean number of H. cordiformis caught per 0.25 m^2 quadrat in each zone each month is shown in Fig. 3-14.

A two-factor analysis of variance (Zones, Times of sampling) was conducted for Zones I, II and III in which all the data were transformed to ln (x+1). Because of the very low numbers of crabs in Zone IV, the data collected for this zone were not included in this analysis. There were significant differences among both Zones and Times of sampling, and no significant Interaction (Table 3-20).

A Student-Neuman-Keul's multiple comparison among the mean numbers of crabs per 0.25 m^2 quadrat in each zone, pooled over the months, showed that the number of crabs was greatest in Zone I, and decreased uniformly and significantly to be least in Zone III (Table 3-20).

Similarly, a Student-Neuman-Keul's multiple comparison for each month, pooled over all zones, indicated that the mean number of crabs was significantly less in the winter months (June and August, 1975) than at all other times of the year (Table 3-20). The mean number of crabs was significantly greater in January, 1976, than in any other month (Fig. 3-14).

FIG. 3-14

Results of photographic census of Heloecius cordiformis. Mean number of crabs per 0.25 m^2 in each zone during each month is shown. No photographic census was taken in May or July, 1975.

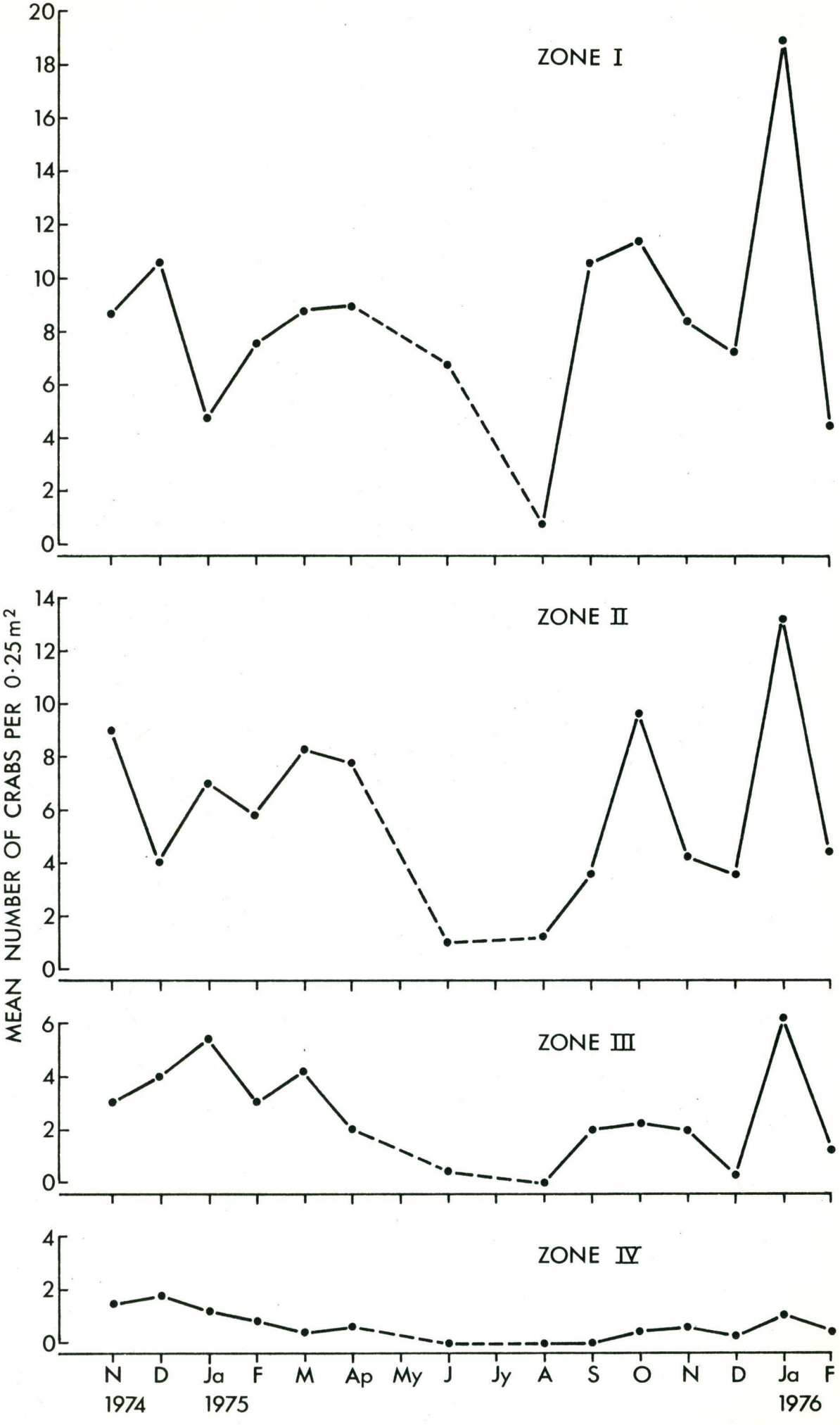

ZONE I
ZONE II
ZONE III
ZONE IV
MEAN NUMBER OF CRABS PER 0·25 m²
N D Ja F M Ap My J Jy A S O N D Ja F
1974
1975
1976

TABLE 3-21

Comparison of numbers of *Sesarma erythrodactyla* and *Australoplax tridentata* sampled in each zone in photographic census.

	Number sampled	Percentage of total number sampled
S. erythrodactyla		
Zone I	12	15
Zone II	22	27
Zone III	24	30
Zone IV	23	28
Total	81	
A. tridentata		
Zone I	56	73
Zone II	20	26
Zone III	1	1
Zone IV	0	0
Total	77	

Sesarma erythrodactyla

S. erythrodactyla were found in all four zones. The smallest numbers occurred in Zone I. Numbers of *S. erythrodactyla* in the other three zones were not significantly different (Table 3-21).

Australoplax tridentata

A. tridentata were only found in Zones I and II, with a single crab found in Zone III (Table 3-21).

3.34 Discussion

Crabs were not evenly distributed vertically up the shore in the study area in the Patonga mangroves. There were two major trends (see Fig. 3-15).

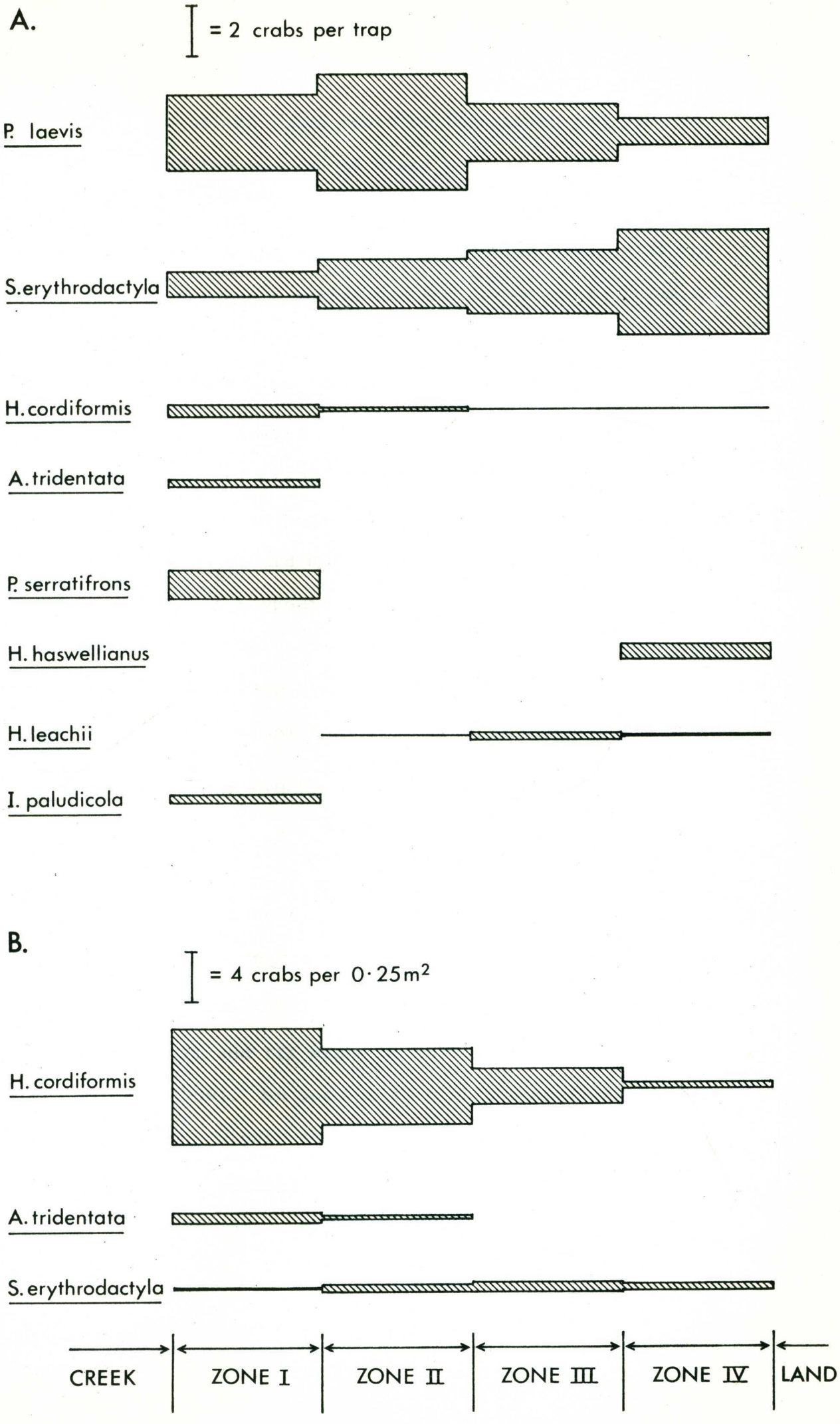
(i) The populations of some species of crabs were confined to the lower levels on the shore (*Pilumnopeus serratifrons*, *Ilyoplax paludicola*) or else were found there in greatest numbers and decreased towards the back of the swamp (*Heloecius cordiformis*, *Australoplax tridentata*.

(ii) The populations of other species of crabs were confined to the back of the swamp (*Helograpsus haswellianus*) or else were found in greatest numbers there and decreased towards the lower levels on the shore (*Sesarma erythrodactyla*).

The exception to these trends was the distribution of *Paragrapsus laevis*, which occurred in greatest numbers towards the middle of the swamp. The position of *Helice leachii* in relation to these trends was unclear because of the small numbers caught. It was absent from the lowest levels of the swamp.

FIG. 3-15

Summary of the distributions of crabs between zones in the mangrove swamp at Patonga: A, from trapping data; B, from photographic censuses.


A.
= 2 crabs per trap
P. laevis
S.erythrodactyla
H.cordiformis
A.tridentata
P. serratifrons
H. haswellianus
H. leachii
I. paludicola
B.
= 4 crabs per 0·25m²
H. cordiformis
A. tridentata
S. erythrodactyla
CREEK
ZONE I
ZONE II
ZONE III
ZONE IV
LAND

Four distinct zones could be identified and defined with respect to the species of crabs present. These four zones corresponded to the four zones into which the study area had been divided on the basis of the relative numbers of the two mangroves Avicennia marina and Aegiceras corniculatum. The distribution and relative abundance of each species of crab over the study area are summarised in Fig. 3-15.

Zone I was lowest on the shore and contained the largest number of species of crabs, namely six. It was characterised by the presence of the xanthid, P. serratifrons, and the grapsid I. paludicola, which did not occur in other zones, and maximum numbers of the two ocypodids, H. cordiformis and A. tridentata. Two other grapsids were also present: S. erythrodactyla, which were present in the lowest numbers of any zone, and P. laevis, which were less abundant than in Zone I.

Zone IV was highest on the shore and contained five species of crabs. It was dominated by grapsids. H. haswellianus was found exclusively in Zone IV, and S. erythrodactyla occurred there in maximal numbers. Other grapsids present in small numbers were H. leachii and P. laevis. Minimal numbers of the ocypodid, H. cordiformis, were also present.

Zones II and III might be termed "transition" zones (cf. Warner, 1969). No species of crab was confined to either of these zones. Significant differences between these zones in the numbers of P. laevis, which were maximum in Zone II (Table 3-12), and of S. erythrodactyla (Table 3-6) and H. cordiformis (Table 3-20B)were used as the basis for identifying these as two separate zones. There were also many more A. tridentata in Zone II than Zone III (Table 3-21).

There is some evidence of variations in the distribution of crabs among the zones. The movement of female S. erythrodactyla from Zones III and IV into Zone II in January, February and March, 1975, was suggested (see page 53). Numbers of gravid S. erythrodactyla were maximal during these months and the greatest percentage of gravid females occurred in Zone II. It is suggested that any movement of female S. erythrodactyla from Zones III and IV into Zone II was a migration of gravid females into a zone lower on the shore to spawn. The subsequent movement of female S. erythrodactyla back into Zones III and IV in April, 1975, was also suggested (see page 53).

The fluctuations in the numbers of P. laevis in Zone IV appeared to be about 3-4 months out of phase with the other three zones (see page 57). It is unlikely that crabs of the same species in different zones would show the greatest levels of activity at different times of the year. The small numbers of P. laevis in Zone IV, at a time when the numbers of P. laevis were at a maximum in the other zones, may indicate a movement of crabs from Zone IV to zones lower on the shore. Such a movement could well be correlated with breeding and spawning by gravid females. Gravid females were present only from May to September, 1975, and this corresponded to the period of maximum numbers in Zones I, II and III. Sampling of larger numbers of P. laevis would be needed to confirm this movement.

Despite the fact that the greatest numbers of P. laevis occurred in Zone II (Fig. 3-8; Table 3-12), 82% of all gravid P. laevis were found in Zone I (Table 3-15). The ratio of male

to female P. laevis over all months in Zones I, II and III was 1:1 (see page 58). It is possible that there was also a migration of gravid P. laevis from Zone II into Zone I to spawn during May to October, 1975 (see Fig. 3-10). There is no direct evidence for this from the trapping data due to the relatively small sample sizes taken each month and the greatest variability in the data for Zone II (see page 56).

Within the zones that have been described above, micro-habitats could be recognised which were occupied by different species of crabs. S. erythrodactyla was the only grapsid seen on the surface at low tide, with the exception of a small number of P. laevis seen on the surface during the study. S. erythro-dactyla were frequently found beneath leaves, fallen timber, inside the entrance of large burrows or around the roots at the base of the mangrove A. marina. When disturbed on the surface, S. erythrodactyla quickly retreated beneath cover (see Section 3.22). Most burrows occupied by S. erythrodactyla were beneath pieces of timber. Where the burrows were on open ground, they were usually situated in depressions in the substratum which retained a higher moisture content at low tide than the raised ground around them. On many occasions S. erythrodactyla were observed climbing mangroves, especially A. marina, possibly to feed on algae growing on the trees or perhaps, to escape predation.

P. laevis were rarely seen on the surface at low tide during the day. They probably remain in burrows during this time. P. laevis were often found beneath oysters or timber in Zone I (see page 41); many of the crabs found there were gravid females, possibly spawning.

The other two grapsids, H. haswellianus and H. leachii, were not seen on the surface at low tide during the day throughout the entire study. It is assumed that they remained in burrows during the day.

The ocypodids all dug burrows and were active on the surface at low tide during the day. They were rarely found beneath leaf litter, timber or other debris, but spent most of the time near their burrows. H. cordiformis were observed feeding and collecting soil and carrying it back to their burrows, as described by Griffin (1968). On some occasions H. cordiformis were seen in large numbers at the water's edge or in the higher levels of the Zostera weed bed when it was exposed to the air. Presumably, they wandered there in search of food. Where the surface of the ground was uneven, burrows of H. cordiformis, in contrast to those of S. erythrodactyla described above, were generally situated on raised areas of the ground.

A. tridentata were usually found on the surface close to their burrows. Some of the burrows of this species had chimneys of soil rising up to 15 mm above the surface of the ground; the crabs inside these burrows were often found to be moulting and had soft carapaces.

I. paludicola were only present in small numbers on the surface at low tide. They live in the soil and among the oysters.

P. serratifrons were found only in Zone I beneath oysters or timber. They were never found in burrows.

Comparison of the size frequency distributions of the crabs sampled indicates that the two smallest species of crabs

present in the study area, A. tridentata and I. paludicola, were principally confined to Zone I (Figs. 3-12, 3-15; Table 3-21). Of two of the larger species of crabs in the study area, S. erythrodactyla and P. laevis, there were greater percentages of smaller crabs in zones lower on the shore (Figs. 3-6, 3-9).

Seasonal changes in the relative abundance of the species of crabs sampled were observed. These variations in relative abundance were caused by: (i) changes in the activity of the crabs at different times of the year, associated with changes in environmental conditions (particularly temperature), feeding requirements of the crabs and breeding seasons, and

(ii) changes in the absolute numbers of crabs present due to death, migration or recruitment of young crabs into the population.

It is probable that changes in the activity of the crabs account for most of the observed seasonal changes in relative numbers of the crabs in samples.

The numbers of most species of crabs increased in the warmer months of the year, reached a maximum in the summer and early autumn, from December to March, and declined to low numbers in winter. The numbers of S. erythrodactyla, H. cordiformis, P. serratifrons, H. leachii and I. paludicola followed this trend (Figs. 3-4, 3-11, 3-13). Changes in the relative abundance of H. cordiformis caught in traps (Fig. 3-11) with those recorded in the photographic census (Fig. 3-14) are fairly consistent. It is significant that gravid female crabs of all these species were found only at times when numbers of crabs were high (Fig. 3-7, Table 3-17). Clearly, changes in the relative

abundance of these species are correlated with both the high temperatures in summer and the onset of breeding seasons.

The exception to this trend was the grapsid, P. laevis. Numbers of P. laevis were greatest in Zones I, II and III in the colder months of May to October, and lowest in the summer months of December, January, and February (Fig. 3-8). Gravid females were only present between May and October (Fig. 3-10). Clearly, seasonal activity of P. laevis is closely associated with breeding season.

Seasonal variations in the numbers of the other two species of crabs caught, A. tridentata and H. haswellianus, are less clear, because small numbers of crabs were caught, and because of the patchiness in the times when they were caught (see pages 61 , 62 ; Table 3-11).

3.4 EXPERIMENTAL INVESTIGATION OF FACTORS AFFECTING THE VERTICAL DISTRIBUTION OF CRABS

3.41 Introduction

It has been suggested by workers in mangrove swamps that various factors might influence the vertical distribution of crabs (see pages 11-14). The major factors that might affect the vertical distribution of crabs in the mangroves at Patonga were considered to be:

(i) salinity of the water,

(ii) properties of the soil: composition of particle sizes; concentration of organic matter; moisture content,

(iii) the period of exposure to air of each zone at low tide, and

(iv) the depth to the water table.

Each of these factors was investigated here. Where differences in them occurred between zones, experiments were conducted to establish to what extent they might be responsible for the observed distribution of crabs.

3.42 Salinity

Salinity is an important factor determining the distribution of crabs along a river (Snelling, 1959; Ono, 1965; Griffin, 1971), but its importance as a determinant of distribution in relation to vertical height on the shore is less clear. Measurements of the salinity of water in the soil at low tide were initially made to establish whether there were differences in the salinity of water in the soil from zone to zone.

TABLE 3-22

Comparison of the salinity of water in the soil in each zone in December, 1974, and April, 1975.

A. Mean salinity (‰) of water in the soil in each zone.

Zone I	Zone II	Zone III	Zone IV
December, 1974			
31.6	32.4	33.8	33.4
April, 1975			
25.0	25.7	20.8	20.0

B. Analyses of variance of the salinity of water in the soil in each zone in December, 1974, and April, 1975.

Source of variation	Sum of squares	Degrees of freedom	Mean square	F-ratio
December, 1974				
Between Zones	23.74	3	7.91	1.68 n.s.
Within Zones	170.02	36	4.72	
Total	193.76	39		
April, 1975				
Between Zones	250.68	3	83.56	21.08**
Within Zones	142.70	36	3.96	
Total	393.38	39		

Zone I Zone II Zone III Zone IV

(i) Measurement of salinity

The null hypothesis that the salinity of water in the soil at low tide did not differ among the four zones was tested.

Materials and Methods.

The mean salinity of water in the soil of each zone at low tide was measured in December, 1974, following a month of relatively low rainfall, and April, 1975, following a month of high rainfall (Table 3-23). On each occasion, 10 holes, each of 10 cm diameter, were dug at random in the soil of each of the four zones at low tide. Each hole was left for 10 minutes while water from the surrounding soil seeped into it. The salinity of the water in each hole was then measured with a salinometer.

Results.

The mean salinities of the water in the soil were lower in April, 1975, than in December, 1974 (Table 3-22A). Single factor analyses of variance of the salinities indicated no significant differences between zones in December, 1974, but significant differences in April, 1975 (Table 3-22B). The mean salinities of the water in the soil of Zones I and II in April, 1975, were significantly higher than in Zones III and IV (S.N.K. test, $P < 0.05$). There was no significant difference between the mean salinities of Zones I and II, nor between the mean salinities of Zones III and IV.

TABLE 3-23

Rainfall data for period of study. Mean (mm) and Standard error (beneath mean) given for each month. (Data supplied by Bureau of Meteorology, Sydney).

1974

F	M	Ap	My	J	Jy	A	S	O	N	D
4.3	8.7	5.4	7.4	6.9	0.5	5.6	1.4	2.3	3.3	0.9
2.7	3.4	1.9	3.1	2.2	0.3	3.1	0.7	0.8	1.0	0.7

1975

J	F	M	Ap	My	J	Jy	A	S	O	N	D
1.3	4.9	12.3	2.5	0.5	11.9	1.5	0.6	1.6	3.5	0.9	1.2
0.5	1.7	6.6	1.2	0.3	4.2	0.8	0.2	0.7	1.2	0.4	0.6

1976

J	F
9.6	8.0
3.4	2.6

(ii) Effect of rainfall on salinity

Rainfall throughout the study was generally high in Autumn and low in Spring and Winter (Table 3-23). Rainfall in Summer varied: it was low in 1974/1975, but high in 1975/1976. Rainfall during December, 1974, when the first salinity readings were taken, and November, 1974, was relatively low (Table 3-23). Rainfall during April, 1975, when the second salinity readings were taken, was nearly three times as great as during December, 1974; rainfall in March, 1975, was the highest recorded during the study.

The lower salinities recorded in all zones in April, 1975, compared to the salinities recorded in December, 1974, (Table 3-22A), were probably the result of dilution by the great amount of rain water which fell in March and April, 1975 (Table 3-23).

The results of the previous section indicate that at times there are some variations between zones in the salinity of water in the soil. These variations in salinity could be due to dilution by rainwater or due to evaporation of water from the surface of the soil. The relative importance of these two factors is unclear.

Evaporation of water from the study area would cause an increase in salinity. Evaporation could cause salinity differences between zones if it was great, and if it differed between zones. Most of the ground in the study area is in shade, which would reduce evaporation during the day. This, and the twice-daily tidal flooding of the study area, would prevent any notable effects of evaporation on the salinity of ground-water.

The reduction in salinity in Zones III and IV during April, 1975, was probably the result of heavy rain, which might be expected to have more effect at the higher levels of the swamp, which are submersed by the tide for shorter periods than the lower levels.

(iii) Experiments on tolerance to salinity

Crabs in the mangroves at Patonga are subject to some differences in salinity among the four zones (Table 3-22). An experiment was, therefore, carried out to determine any differences in mortality among the four most abundant species of crabs as a result of differences in tolerance to various salinities. Salinities of 15‰, 25‰ and 33‰ were selected to span the range of salinities experienced in the swamps. A salinity of 16‰ was the lowest recorded in the mangrove swamp. This was recorded in April, 1975, following the month in which rainfall was the highest during the study (Table 3-23).

The null hypothesis that crabs of the four species, Sesarma erythrodactyla, Paragrapsus laevis, Heloecius cordiformis and Australoplax tridentata survived equally well in water of salinities of 15‰, 25‰ and 33‰ was tested.

Materials and Methods

Ten crabs of each species were placed in individual, covered plastic containers (15 cm x 15 cm x 9 cm high) filled with water at one of the three salinities of 15‰, 25‰ and 33‰. The water was aerated and the crabs were not fed throughout the 14 days of the experiment. The containers were inspected daily and dead crabs removed.

TABLE 3-24

Results of experiment on tolerance of *Sesarma erythrodactyla*, *Paragrapsus laevis*, *Heloecius cordiformis* and *Australoplax tridentata* to water of three salinities. (10 crabs of each species placed in water of each salinity)

	Number of crabs alive after 14 days.		
	15%	25%	33%
S. erythrodactyla	10	10	10
P. laevis	9	10	10
H. cordiformis	10	9	10
A. tridentata	9	10	10

Results

Only 3 of the total number of 120 crabs died throughout the 14 days exposure to the experimental salinities (Table 3-24). The results clearly demonstrate that all four species were extremely tolerant of the salinities encountered.

3.43 Composition of Particle Sizes of the Soil

The composition of particle sizes of the soil might affect the distribution of crabs because of its effect on:

(i) the ability of the soil to retain moisture,

(ii) the suitability of the soil as a place in which to dig burrows, and

(iii) the suitability of the soil for feeding, especially by ocypodids (Crane, 1941, 1975; Ono, 1965; Macnae, 1968; Griffin, 1971).

The null hypothesis that the composition of particle sizes of the soil did not differ over the four zones was tested.

Materials and Methods.

Five soil samples from the top 10 cm of soil were collected at random from each zone. These were analysed by a hydrometer method (Black, 1965) in which hydrometer readings were taken after 5 minutes and 8 hours. The particles were grouped according to International sizes (Intern. Soc. Soil Sc., 1929). The relative percentages of clay (diameter of particles < 0.002 mm), silt (diameter of particles between 0.002 mm and 0.02 mm), fine sand (diameter of particles between 0.02 mm and 0.2 mm) and coarse sand (diameter of particles > 0.2 mm) were determined in each sample.

TABLE 3-25

Comparison of the composition of particle sizes of the soil in each zone.

A. Mean percentage of particles of each size in each zone

	Clay (0.002 mm)	Silt (0.002-0.02 mm)	Fine Sand (0.02-0.2 mm)	Coarse sand (0.2 mm)
Zone I	6.7	5.1	1.3	86.9
Zone II	4.2	3.8	0.9	91.1
Zone III	3.5	4.0	0.9	91.6
Zone IV	3.7	3.8	0.7	91.8

B. Analysis of variance of percentages of fine particles (silt, clay, fine sand) in the soil in each zone (all data transformed to arc sine).

Source of variation	Sum of squares	Degrees of freedom	Mean square	F-ratio
Between Zones	59.41	3	19.80	12.80**
Between Sizes of particles	546.52	2	273.26	176.67**
Interaction: Zones x Sizes of particles	15.37	6	2.56	1.66 n.s.
Residual	74.24	48	1.55	
Total	695.54	59		

Zone I Zone II Zone III Zone IV

Results.

The mean percentage of particles of each size in each zone is shown in Table 3-25A. A two-factor analysis of variance indicated significant differences among zones and among percentages of different particle sizes (Table 3-25B). There was no interaction between these two variables. Zone I had significantly greater percentages of the finer fractions (clay, silt and fine sand) than Zones II, III and IV, which were not significantly different from one another (S.N.K. test, $P = 0.05$).

3.44 Concentration of Organic Matter in the Soil

Organic matter in the soil is the food for many species of crabs, especially ocypodids (Crane, 1941, 1975; Ono, 1965; Macnae, 1968; Griffin, 1971). Clearly, differences in the concentration of organic material in the soil between zones might be an important factor influencing the vertical distribution of crabs in the mangroves at Patonga.

The null hypothesis that there was no difference in the concentration of organic matter in the soil between zones was tested.

(i) Determination of concentration of organic matter by titration.

Materials and Methods

Five soil samples from the top 10 cm of soil were collected at random from each zone. The organic carbon content of each soil sample was analysed according to Tinsley's method of titration with acid-dichromate solution (Tinsley, 1950). The percentage organic matter was then estimated using the equation

TABLE 3-26

Comparison of the concentration of organic matter in the soil in each zone (as determined by titration)

A. Mean percentage organic matter in the soil

	Zone I	Zone II	Zone III	Zone IV
Mean % organic matter	2.48	2.30	1.87	2.82

B. Analysis of variance of percentages of organic matter in the soil in each zone

Source of variation	Sum of squares	Degrees of freedom	Mean square	F-ratio
Between Zones	0.77	3	0.26	1.28 n.s.
Within Zones	3.21	16	0.20	
Total	3.98	19		

$$\% \text{ organic matter} = \% \text{ organic carbon} \times \frac{100}{57}$$

since on average organic matter in soil contains 57% carbon (Black et al., 1965).

Results.

The mean percentage of organic matter in the soil in each zone is shown in Table 3-26A. A single factor analysis of variance indicated no significant difference in the mean percentage of organic matter between the four zones (Table 3-26B). The amounts of organic matter measured seemed rather low when considered in relation to the seemingly large amounts of fine tangled mangrove roots present in the soil in the study area. It is possible that some of the larger pieces of organic matter may not have been completely digested by the acid/dichromate solution. A second determination of the organic matter present in each zone was therefore made using a different method.

(ii) Determination of concentration of organic matter by heating to ignition point.

Materials and Methods.

Three soil samples were collected at random from the top 10 cm of soil in each zone. The organic matter present in each sample was determined by heating to ignition point (Black et al., 1965).

1.5 g of each soil sample was oven-dried at 105°C until constant weight was attained. Each sample was then placed in an oven at 500°C, until constant weight was attained. The loss of weight when heated to 500°C was calculated as a percentage of the oven dry weight at 100°C. This loss of weight represented

TABLE 3-27

Comparison of the concentration of organic matter in the soil in each zone (as determined by heating to ignition point).

A. Mean percentage organic matter in the soil

	Zone I	Zone II	Zone III	Zone IV
Mean % organic matter	3.46	3.43	2.33	3.56

B. Analysis of variance of percentages of organic matter in the soil in each zone.

Source of variation	Sum of squares	Degrees of freedom	Mean square	F-ratio
Between Zones	3.01	3	1.00	3.02 n.s.
Within Zones	2.65	8	0.33	
Total	5.66	11		

organic matter in the soil which ignited on heating at 500°C.

This method of determination of organic matter was considered justifiable because of the low clay content of the soil in the study area (maximum mean clay content 5.1%, see Table 3-25A). This meant that there would be little water stored in the soil and released at 500°C, that was not released at 100°C (Black et al., 1965).

Results.

The mean percentage of organic matter in each zone is shown in Table 3-27A. A single factor analysis of variance indicated that there was no significant difference in the mean percentage of organic matter between zones (Table 3-27B).

The mean percentages of organic matter in each zone were consistently higher when determined by this method than those determined by Tinsley's titration method. This is probably due to the incomplete digestion by the acid/dichromate solution of larger pieces of organic matter in the former method, as discussed previously.

3.45 Depth to the Water Table.

The depth from the surface of the soil to the water table at low tide could influence the distribution of crabs in two ways: (i) it determines the depth to which a crab must burrow to reach water at low tide and (ii) it affects the moisture content of the soil.

The null hypothesis that the depth from the surface of the soil to the water table at low tide did not vary between zones was tested.

TABLE 3-28

Comparison of the depth to the water table in each zone.

A. Mean depth to the water table in each zone

	Zone I	Zone II	Zone III	Zone IV
Mean depth to water table (mm)	46.0	76.0	136.0	142.5

B. Analysis of variance of depths to water table in each zone.

Source of variation	Sum of squares	Degrees of freedom	Mean square	F-ratio
Between Zones	65941.88	3	21980.63	17.67**
Within Zones	44782.50	36	1243.96	
Total	110724.38	39		

Zone IV Zone III Zone II Zone I

Materials and Methods.

Ten holes, each of 10 cm diameter, were dug at random in the soil of each of the four zones. Each hole was left until the level of water in it became steady. The distance from the surface of the soil to the surface of the water in the hole was measured.

Results.

The mean depth to the water table in each zone is shown in Table 3-28A. A single factor analysis of variance indicated that there were significant differences between the depths to the water table (Table 3-28B). The depth to the water table was significantly greater in Zones III and IV than in Zones I and II (S.N.K. test, $P < 0.05$). There was no significant difference between zones I and II, nor between Zones III and IV (S.N.K. test, $P > 0.05$).

3.46 Moisture Content of the Soil.

The moisture content of the soil affects the humidity of the air above the surface of the soil at low tide. Increased evaporation of water from soil of high moisture content would raise the humidity of the air above the soil. If the moisture content of the soil was very low it might reduce the humidity of the air above the soil to levels at which crabs on the surface of the soil might face problems of desiccation. The moisture content of the soil may also affect the suitability of the soil as a place in which crabs of different species can dig burrows. Thus, variations in moisture content of the soil between zones could affect the distribution of crabs in the study area.

TABLE 3-29

Comparison of the moisture content of the soil in each zone.

A. Mean percentage moisture content of soil in each zone (calculated as % of dry weight of soil).

	Zone I	Zone II	Zone III	Zone IV
Mean % moisture content	20.68	19.45	17.86	19.12

B. Analysis of variance of percentage moisture content of soil in each zone.

Source of variation	Sum of squares	Degrees of freedom	Mean square	F-ratio
Between Zones	40.18	3	13.39	13.20**
Within Zones	36.52	36	1.01	
Total	76.70	39		

Zone I Zone II Zone IV Zone III

The null hypothesis that the moisture content of the soil did not vary between zones was tested.

Materials and Methods.

Ten samples of soil were collected at random from the top 10 cm of each zone at low tide. The samples were returned to the laboratory in sealed containers. 30 g of the soil from each sample was heated in an oven at 105^{o}C until constant weight was attained. The weight loss was calculated as a percentage of the final dry weight of the sample. The weight loss was due to the moisture lost by the sample during heating.

Results.

The mean percentage moisture content of the soil in each zone is shown in Table 3-29A. A single factor analysis of variance indicated that there were significant differences between the moisture contents of the zones (Table 3-29B). The moisture content of the soil in Zone I was significantly greater than the moisture contents of the soil in Zones II and IV, which were not significantly different from each other. The moisture content of the soil in Zone III was significantly lower than the moisture content of the soil in the other three zones (S.N.K. tests, $P = 0.05$).

3.47 Tolerance to Different Humidities.

Some of the species of crabs present in the mangrove swamp at Patonga spend a great deal of time on the surface of the soil at low tide during the day (Section 3.34). Differences in the tolerances of different species of crabs to different

humidities might be important in determining the vertical distribution of the crabs.

The principal factor influencing the humidity of the air above each zone is the period of time for which each zone is exposed to air. This is first discussed here, before experiments on the tolerance of crabs to different humidities are described.

(i) Period of exposure to air

It is obvious that zones higher on the shore are exposed to air for a longer time than zones lower on the shore. The time for which each zone was exposed to air was measured on a single occasion (in October, 1976) to give some information on the relative times of exposure to air of each zone.

As well as influencing the humidity of the air above the soil in each zone, the period of exposure to air may be important because it determines the time for which crabs can feed on the surface at low tide.

Materials and Methods.

The time taken for the water to rise from the level at low tide and to reach the middle of each zone in turn was recorded and used to estimate the time of exposure to air during low tide of each zone.

At low tide three markers were placed 20 m apart across the middle of each zone. As the tide rose, the time taken by the water to reach each marker from low tide level was recorded. The mean time from low tide at which the rising tide reached the middle of each zone was calculated. This time was doubled to provide an estimate of the mean time for which the middle of each

TABLE 3-30

Mean time of exposure to air of middle of each zone

	Zone I	Zone II	Zone III	Zone IV
Mean time of exposure (hr)	3.56	6.26	9.10	10.26

zone was exposed to air. The assumption was made that the rate of fall of water during the ebbing tide equalled the rate of rise as the tide came in.

Results.

Estimates of the mean time for which the middle of each zone was exposed to the air are given in Table 3-30. The largest zone, Zone III, was exposed to air for 2.6 times as long as Zone I and 1.5 times as long as Zone II. Zone II was exposed to air for 1.8 times as long as Zone I. The zone highest on the shore, Zone IV, was exposed to air for the longest time, but only 1.1 times as long as Zone III.

(ii) Experiments on tolerance to different humidities.

The times for which crabs of four species could survive in different humidities were investigated. The tolerance of a species to a particular humidity was thus defined as the mean length of time before death.

The null hypothesis that Sesarma erythrodactyla, Paragrapsus laevis, Heloecius cordiformis and Australoplax tridentata were equally tolerant to relative humidities of 20%, 45%, 76% and 100% was tested.

Materials and Methods.

Four series of four containers were maintained at internal humidities of 20%, 45%, 76% and 100%, respectively. Each container was 15 cm in diameter and 18 cm high and contained a stainless steel wire mesh platform supported on three 4 cm high perspex legs. Each was fitted with an airtight lid. All containers were kept

TABLE 3-31

Comparison of the tolerances of *Sesarma erythrodactyla*, *Paragrapsus laevis*, *Heloecius cordiformis* and *Australoplax tridentata* to three humidities.

A. Mean length of time (hr) before death of each species in three humidities.

Humidity	*S. erythrodactyla*	*P. laevis*	*H. cordiformis*	*A. tridentata*
20%	16.33	15.00	13.00	7.67
45%	21.67	11.33	16.33	9.00
76%	39.00	49.00	39.00	19.67

B. Analyses of variance of lengths of time (hr) before death of each species in three humidities. All data transformed to $\sqrt{\text{time} + 1}$.

Source of variation	Sum of squares	Degrees of freedom	Mean square	F-ratio
20% humidity				
Between Species	7.42	3	2.47	4.87**
Within Species	16.25	32	0.51	
Total	23.67	35		
45% humidity				
Between Species	14.75	3	4.92	7.34**
Within Species	21.44	32	0.67	
Total	36.19	35		
76% humidity				
Between Species	28.14	3	9.38	6.20**
Within Species	48.44	32	1.51	
Total	76.58	35		

S.N.K. tests:

20% humidity

S. erythrodactyla *P. laevis* *H. cordiformis* *A. tridentata*

45% humidity

S. erythrodactyla *H. cordiformis* *P. laevis* *A. tridentata*

76% humidity

P. laevis *S. erythrodactyla* *H. cordiformis* *A. tridentata*

in a constant temperature room at 20 ± 5°C.

Humidities of 20%, 45% and 76% were created by placing to a depth of 2 cm in the bottom of the containers saturated solutions of potassium acetate, sodium carbonate and sodium chloride, respectively (Winston and Bates, 1960). The fourth container in each series was used as a control and contained 2 cm of distilled water to create a relative humidity of 100%.

Nine crabs of each species were placed in each humidity. This number was limited by the difficulty of catching P. laevis on the surface. The crabs of each species that were used were of approximately the same size. Crabs were not fed during the experiment.

After the containers had been set up with crabs at the beginning of each trial, they were examined every six hours and the dead crabs in each counted and then removed. This was repeated until all crabs in the containers of 20%, 45% and 76% humidities had died. The time of death of each crab was recorded as the mid-point between the time at which it was found to be dead and the time of the previous inspection of its container when it was alive. The recorded time of death was thus within three hours of the actual time of death.

Results.

The results of the experiments on tolerance to different humidities are shown in Table 3-31. No crab in the control containers of 100% humidity died throughout the experiments. Deaths of crabs in the other containers could thus be directly attributed to the different humidities in these containers. Analyses of

variance of the lengths of time before death (= tolerances) of the four species in each humidity were done (Table 3-31A). A. tridentata was the least tolerant in each of the three humidities, while S. erythrodactyla and H. cordiformis were equally tolerant in each humidity. P. laevis was as tolerant as S. erythrodactyla and H. cordiformis in 20% and 76% humidities, but less tolerant in 45% humidity.

3.48 Experiments on Preference for Type of Soil and Moisture Content of Soil.

The preferences shown by crabs of different species for soils from Zone I and Zone II, and for soils with high and low moisture content were tested. These experiments determined any differences between the species in their responses to environmental variables related to the soil in different parts of the study area.

Materials and Methods.

Four plastic tanks 100 cm x 50 cm x 40 cm deep were filled at one end with soil removed from Zone I. The other end was filled with soil from Zone II. The soil was removed by spade from the floor of the mangrove swamp in large blocks and immediately placed into the tanks. It was disturbed as little as possible. Throughout the experiments the tanks were kept in the laboratory in a constant temperature room at 20 $\pm$ 5^{o}C. Each tank thus contained soil representing the two soil types available to crabs in the Patonga mangroves: soil from Zone I, with a significantly greater proportion of finer particles, and soil from Zone II, which was of the same composition of particle sizes as soil in Zones III and IV (Table 3-25).

Two of the tanks were tilted to an angle of 15° so that the soil from Zone I was raised. The other two tanks were tilted to the same angle so that the soil from Zone II was raised. The tanks were left for two days. During this time seawater was poured over the soil in the lower half of each tank to maintain a high soil moisture content without letting any pools of seawater collect. One quarter of this volume of seawater was poured over the soil in the raised end of each tank. The smaller volume of added water and the increased drainage from the raised ends of the tanks ensured that the soil there retained a lower moisture content than the soil in the lower ends. Two of the tanks thus contained soil of high moisture content from Zone I and soil of low moisture content from Zone II; the other two tanks contained soil of low moisture content from Zone I and soil of high moisture content from Zone II.

Each species of crab was tested separately. Crabs were released in the centre of each of the four tanks at the junction of the two soil types and left in the tanks for 24 hours. The positions in which they had settled after this time and the positions of any burrows that had been dug were noted. The crabs were then removed and burrows that had been dug filled in. Seawater was then added to each tank as described above and a new group of crabs tested.

Eighty seven Sesarma erythrodactyla were tested in groups of 5 crabs or fewer per tank; 72 Heloecius cordiformis in groups of 6 per tank; 120 Australoplax tridentata in groups of 5 per tank; 80 Paragrapsus laevis in groups of 4 per tank.

TABLE 3-32

Results of experiments on preferences of *Sesarma erythrodactyla* *Paragrapsus laevis*, *Heloecius cordiformis* and *Australoplax tridentata* for composition of particle size of soil and moisture content of soil.

A. Number of crabs settling on each set of soil conditions

Origin of Soil:	Zone I	Zone I	Zone II	Zone II
Moisture content of soil:	high	low	high	low
S. erythrodactyla	32	2	39	14
P. laevis	40	0	40	0
H. cordiformis	30	3	33	6
A. tridentata	59	2	58	1

B. Values of X^2 in analyses of numbers of crabs of each species settling on soil from Zone I and Zone II.

S. erythrodactyla	4.15^{*}
H. cordiformis	0.50 n.s.
A. tridentata	0.04 n.s.

C. Values of X^2 in analyses of numbers of crabs of each species settling on soil of high and low moisture content.

S. erythrodactyla	34.77^{**}
H. cordiformis	40.50^{**}
A. tridentata	108.30^{**}

Results.

Table 3-32A shows the numbers of crabs of each species that settled in each set of conditions of soil type and moisture content. Chi-squared tests were done on the results for each species, except P. laevis, to detect any significant differences in the numbers of crabs that settled on either soil type and in soil of either moisture content. (Table 3-32B). No formal analyses of the results for P. laevis were required.

Sesarma erythrodactyla

A significantly greater number of crabs settled in soil of high rather than low moisture content (Table 3-32; $P < 0.01$). In addition, significantly more crabs settled in soil from Zone II than in soil from Zone I (Table 3-32; $P < 0.05$). Thus crabs of this species showed a strong preference for soil of high moisture content, and a weaker preference for soil from Zone II.

Throughout the trials only eight burrows were dug. These were 3 cm or less deep, except for one burrow that was 10 cm deep. Most crabs settled in small depressions in the mud against the sides of the tanks, often huddled in groups of 4 or 5 individuals.

Paragrapsus laevis

Crabs of this species only settled on the soil with high moisture content. They thus showed an absolute preference for soil of high moisture content, regardless of the origin and composition of the soil.

Seventeen burrows were dug throughout the trials, but most were little more than shallow depressions scooped out of the soil. The deepest burrow reached a depth of 8 cm.

Heloecius cordiformis

Significantly more crabs settled in soil of high rather than low moisture content (Table 3-32; $P < 0.01$). There was no significant difference in the numbers of crabs settling in the soils of each type. Thus, crabs of this species showed a strong preference for soil of high moisture content, but no preference between soils of different composition of particle sizes.

The 72 H. cordiformis dug 101 burrows; many crabs dug more than one burrow. Thirty-nine of these burrows had entrances covered by plugs of soil; each of these covered burrows was occupied by a crab. Burrows ranged in depth from shallow depressions barely large enough to hide the crab below the surface of the soil, to vertical holes up to 10 cm deep. All were dug vertically, with the exception of one burrow that had been dug vertically for 5 cm and then horizontally a further 6 cm. 81% (81 out of 101) of these burrows were dug in the soil of high moisture content.

Australoplax tridentata

As with H. cordiformis, a significantly greater number of crabs settled in soil of high rather than low moisture content (Table 3-32; $P < 0.01$), and there was no significant difference between the numbers of crabs settling in the two types of soils. Thus, crabs of the species A. tridentata showed a strong preference for soil of high moisture content, but no preference between soils of different particle size composition.

Only 10 burrows were dug by crabs of this species. All were very shallow; the maximum depth was 3 cm.

3.49 Discussion

Four of the factors that were discussed in the General Introduction (pages 11-13) were not considered to be important in influencing the distribution of crabs on the shore at Patonga and were not tested. These were temperature, the hydrogen-ion concentration of the water, predation and interspecific interactions. These are further discussed on pages 125, 126.

Two of the factors that were tested have no effect on the vertical distribution of crabs on the shore in the mangroves at Patonga. First, the concentration of organic matter in the soil did not vary between zones (Tables 3-26, 3-27). It might be expected that the concentration of organic matter would be greater in Zone I than in the other three zones. Zone I contained a significantly greater percentage of finer particles in the soil (Table 3-25) and the organic matter in intertidal soils generally increases as the percentage of finer particles increases (Newell, 1970). The relatively low concentration of organic matter in the soil in Zone I might be due to the absence of mangrove trees from this zone. Second, although there was some variability between zones in the salinity of water in the ground, crabs of the four species investigated were able to survive for long periods over the range of salinities likely to be found in the field.

The composition of particle sizes of the soil could have some influence on crab distribution. The substratum in the mangroves at Patonga has a very high concentration of coarse sand; the mean percentage of coarse sand is around 90% (Table 3-25). This is further discussed on page 115.

The significantly greater percentages of finer fractions in the soil in Zone I (Table 3-25) might be important in determining differences in the distribution of crabs between Zone I and the other three zones. Clearly, however, any differences in the distributions of crabs in Zones II, III and IV cannot be attributed to differences in the composition of the soil in these three zones.

The moisture contents of the soil in Zones I, II and III (Table 3-29) are consistent with the trends in the depth to the water table in each of these zones (Table 3-28). They are also correlated with the period for which each zone is exposed to the air (Table 3-30). The greater moisture content of the soil in Zone I is also consistent with the greater percentage of finer fractions in the soil in that zone (Table 3-25). Finer particles in the soil would be expected to retain a greater amount of moisture than coarser particles. The moisture content of the soil in Zone IV is unexpectedly high. This zone might be expected to have the lowest soil moisture content: it is exposed to air for the longest time (Table 3-30) and the surface of the soil is further from the water table than in other zones (Table 3-28). The size composition of particles in Zone IV is not significantly different from those in Zones II and III (Table 3-25). The reason for the high moisture content of the soil in Zone IV is unknown.

Moisture content of the soil appears to be the most important factor influencing the vertical distribution of three species of crabs.

Australoplax tridentata were least tolerant of low humidities (Table 3-31) and showed an absolute preference for soil of high moisture content, regardless of the size of the particles (Table 3-32). It is significant that this is the smallest of the species tested and therefore has the greatest surface area: volume ratio. It has been shown that small crabs lose water more quickly than large crabs (Verwey, 1930). As well, A. tridentata spend a great deal of time at low tide on the surface of the soil, which they sift through their mouth-parts to obtain food. Results of the experiments on tolerance to humidity indicate that if A. tridentata were exposed to humidities as low as those tested in this experiment (i.e. 46% and 20%) for times of the order of those for which Zones III and IV are exposed to the air (Table 3-30) they would not survive. These results are consistent with the distribution of A. tridentata: they are found principally in Zone I, with only very small numbers in other zones (Fig. 3-15).

The second ocypodid, Heloecius cordiformis, showed a preference for soil of high moisture content, regardless of the size of the soil particles (Table 3-32). The occurrence of H. cordiformis in greatest numbers in those zones lower on the shore is consistent with these results (Fig. 3-15). Soil moisture content is probably the important factor determining the distribution of H. cordiformis in the study area.

Composition of particles sizes of the soil is probably not important in determining the distribution of H. cordiformis in the study area. H. cordiformis showed no special preference for soil of either composition of particle sizes in the pre-

ference experiments. Griffin (1971) examined the mouthparts of H. cordiformis and found that they have both broad-spooned hairs, enabling them to feed in dry sandy muds, and "woolly" hairs, enabling them to feed in wet muds of high clay content. Thus, H. cordiformis can probably feed equally well on the two types of soil present in the study area. In addition, in the preference experiments and in the field, H. cordiformis appeared to be able to dig burrows equally well in either type of soil.

Despite having a preference for soil of high moisture content, H. cordiformis are well able to spend extended periods of time on the surface of the soil, as they do at low tide, especially during the summer months. They were more tolerant of reduced humidities than A. tridentata; the mean time for which they survived in the lowest experimental humidity tested (20%) greatly exceeded the time for which any zone on the shore was exposed to air at low tide (Tables 3-30, 3-31). Griffin (1971) showed that the volume of the gills of H. cordiformis is low in relation to the total volume of the body of the crab, a feature characteristic of species which spend a good deal of time out of water (Edney, 1960). Griffin (1971) also found that when H. cordiformis were given the choice of settling beneath water or on soil exposed to air, they showed a strong preference to settle out of water.

The greatest numbers of H. cordiformis were present on the lower levels on the shore and dug burrows there in the soil which is of high moisture content. H. cordiformis present on higher levels on the shore often dug burrows on raised parts of the surface of the soil, rather than in the more moist depressions

in the soil. The reason for this is unclear. It may be the result of competition for space with the grapsids, Sesarma erythrodactyla and Paragrapsus laevis. The entrances to burrows of these two species often occupied the moist depressions in the soil.

S. erythrodactyla showed a preference to settle on soil of high moisture content (Table 3-32); they might, therefore, be expected to occur in greatest numbers on those zones lower on the shore (cf. Table 3-29). The distribution of S. erythrodactyla, however, shows the opposite trend; its numbers increase towards the higher levels on the shore. The moisture content of the soil is thus not the most important factor determining the vertical distribution of this species, although it possibly influences the occurrence of greater number of smaller crabs in Zone I (Fig. 3-6; Verwey, 1930).

S. erythrodactyla appear to be well adapted to cope with whatever problems of desiccation they may encounter by living on higher levels on the shore. S. erythrodactyla were as tolerant of reduced humidities as H. cordiformis and the mean time for which they survived in the lowest experimental humidity tested (i.e. 20%) exceeded the time for which any zone on the shore is exposed to air at low tide (Tables 3-30, 3-31). The adaptations of grapsids to breathing air have been described by a number of workers. The outer walls of the branchial region are modified to form reticulated surfaces for aeration of exhalent water, so that the same water can be used again for bathing the gills (Verwey, 1930; Edney, 1960; Macnae, 1968). The tendency of crabs of this species to remain beneath cover during the day

at low tide and to be most active at night, the digging of burrow entrances in areas of high moisture (i.e. beneath timber or in depressions in the ground) and the occupation of extensive networks of tunnels beneath the floor of the swamp, further reduce the chances of desiccation.

S. erythrodactyla showed a preference to settle on soil from Zone II (which is not significantly different in particle-size composition from Zones III and IV; Table 3-25), rather than Zone I. The composition of particle sizes of the soil may, therefore, restrict the greatest numbers of S. erythrodactyla to Zones II, III and IV. This is unlikely, however, since it does not account for the fact that the numbers of S. erythrodactyla increase consistently from Zone I up the shore to Zone IV.

Clearly, more research is needed to determine the most important factors influencing the vertical distribution of S. erythrodactyla. The suitability of the soil as a place in which they can dig networks of burrows may be important, as might the greater time available for crabs to scavenge for food during low tide on the higher zones on the shore.

Paragrapsus laevis were as tolerant of humidities of 76% and 20% as S. erythrodactyla and H. cordiformis, but less tolerant of 45% humidity in which they survived for the same time as A. tridentata (Table 3-31). The ability of P. laevis to withstand desiccation is possibly greater than that of A. tridentata but less than that of S. erythrodactyla and H. cordiformis. The mean time for which P. laevis survived in the lowest humidities tested (i.e. 20%) exceeded the time for which any zone on the shore is exposed to air at low tide

(Tables 3-30, 3-31). P. laevis showed a preference for soil of high rather than low moisture content, but no preference between soils of different composition of particle size (Table 3-32). The presence of the greatest numbers of P. laevis in Zones I and II, and smaller numbers in Zones III and IV is consistent with these results. Moisture content of the soil appears to be an important factor influencing the vertical distribution of this species. The nocturnal behaviour of P. laevis, the tendency to remain beneath cover during the day during low tide, adaptation to aerial breathing (see page 93), and the restriction of the period of greatest activity to winter months, would greatly help P. laevis resist desiccation in the field.

Thus, it appears that the moisture content of the soil is an important factor determining the vertical distribution of H. cordiformis, A. tridentata and P. laevis on the shore at Patonga. Factors determining the distribution of S. erythrodactyla are, however, less clear.

SECTION 4. REPRODUCTIVE BIOLOGY OF MANGROVE CRABS

4.1 INTRODUCTION

No studies have been published on the reproductive biology of any of the species of crabs present in the study site in the Patonga mangroves. The only information available gives some data on times when some of the species have been observed to be gravid (Griffin, 1971; Green and Anderson, 1973). As a complete understanding of the reasons for seasonal fluctuations in the numbers of crabs, or movements of crabs between zones, is not possible without a knowledge of the reproductive cycles of the crabs, an investigation of these was undertaken here.

The aims of this section were:

(i) to identify changes in the reproductive condition of female crabs of the most abundant species by histological examination of the ovaries and to correlate these with changes in the external appearance of the ovaries, and

(ii) to identify any seasonal changes in the condition of the male reproductive system of the most abundant species of crabs by external examination of the gonads.

The reproductive biology of three species of crab (Sesarma erythrodactyla, Paragrapsus laevis and Heloecius cordiformis) was studied in detail. Changes in the condition of the ovaries of Australoplax tridentata were studied by external examination of monthly samples, but lack of time in the present study precluded a detailed histological examination of this species.

Changes in the male reproductive systems of S. erythrodactyla, P. laevis, H. cordiformis and A. tridentata were investigated by external examination of the gonads in samples collected at monthly intervals.

4.2 MATERIALS AND METHODS

Samples were collected at monthly intervals from the Patonga mangroves from February, 1974, to May, 1975, and in July and September, 1975. Five male and five female crabs of each of the species Sesarma erythrodactyla, Paragrapsus laevis, Heloecius cordiformis and Australoplax tridentata were collected on each occasion. The crabs were collected by hand from the surface, from beneath oysters and fallen timber or removed from burrows. They were collected from areas immediately adjacent to the study area, not from the study area itself. This was done to avoid the effects that regular removal of crabs from the study area might have on the sampling programme.

The crabs were kept unfed in aerated seawater in laboratory tanks overnight. They were then dissected under a microscope. The features of each female crab recorded were:

(i) maximum carapace width,

(ii) the appearance and maximum diameter of any eggs attached externally to the ventral surface of the abdomen,

(iii) the appearance and size of the ovaries,

(iv) the appearance and maximum diameter of oocytes within the ovaries, and

(v) the appearance and diameter of the spermathecae.

The features of each male crab recorded were:

(i) maximum carapace width,

(ii) the appearance and size of the testes, and

(iii) the appearance and width of the vas deferens.

The anterior part of one ovary of each female crab, of species S. erythrodactyla, P. laevis and H. cordiformis, was removed and fixed overnight in 10% formalin in seawater. Smith's formol-bichromate was initially tested as fixative but caused considerable shrinkage of mature oocytes. Little shrinkage of oocytes occurred with 10% formalin in seawater. Following dehydration, in a graded series of alcohols, specimens were cleared in amyl acetate, impregnated in paraffin wax ($56^{o}C$) overnight and embedded in paraffin wax. Sections of each specimen were cut at a thickness of 10 μm. All sections were stained with Heidenhain's iron-haematoxylin (for 10 minutes at $56^{o}C$), using 4% iron alum as mordant, and mounted in Eukitt mounting medium. No counterstain was used.

After general examination of each slide individual sections at intervals of 100 to 150 μm along the 1 mm length of tissue sectioned were examined in detail at a magnification of x 80. Three sections were examined on each of three slides for each crab. Three crabs of each species were examined in this way. Thus, a total of 9 sections of each crab, and 27 sections for each species of crab, were examined each month. The following details were recorded from each section:

(i) the numbers of mature and immature oocytes (defined on page 103) in a fixed field of view defined by two parallel lines marked

on the microscope eyepiece,

(ii) the diameters of the first 10 mature oocytes as seen from the right hand side of the field of view, and

(iii) the presence or absence of oogonia.

The mean percentage of mature oocytes and the mean diameter of mature oocytes were calculated for each species each month.

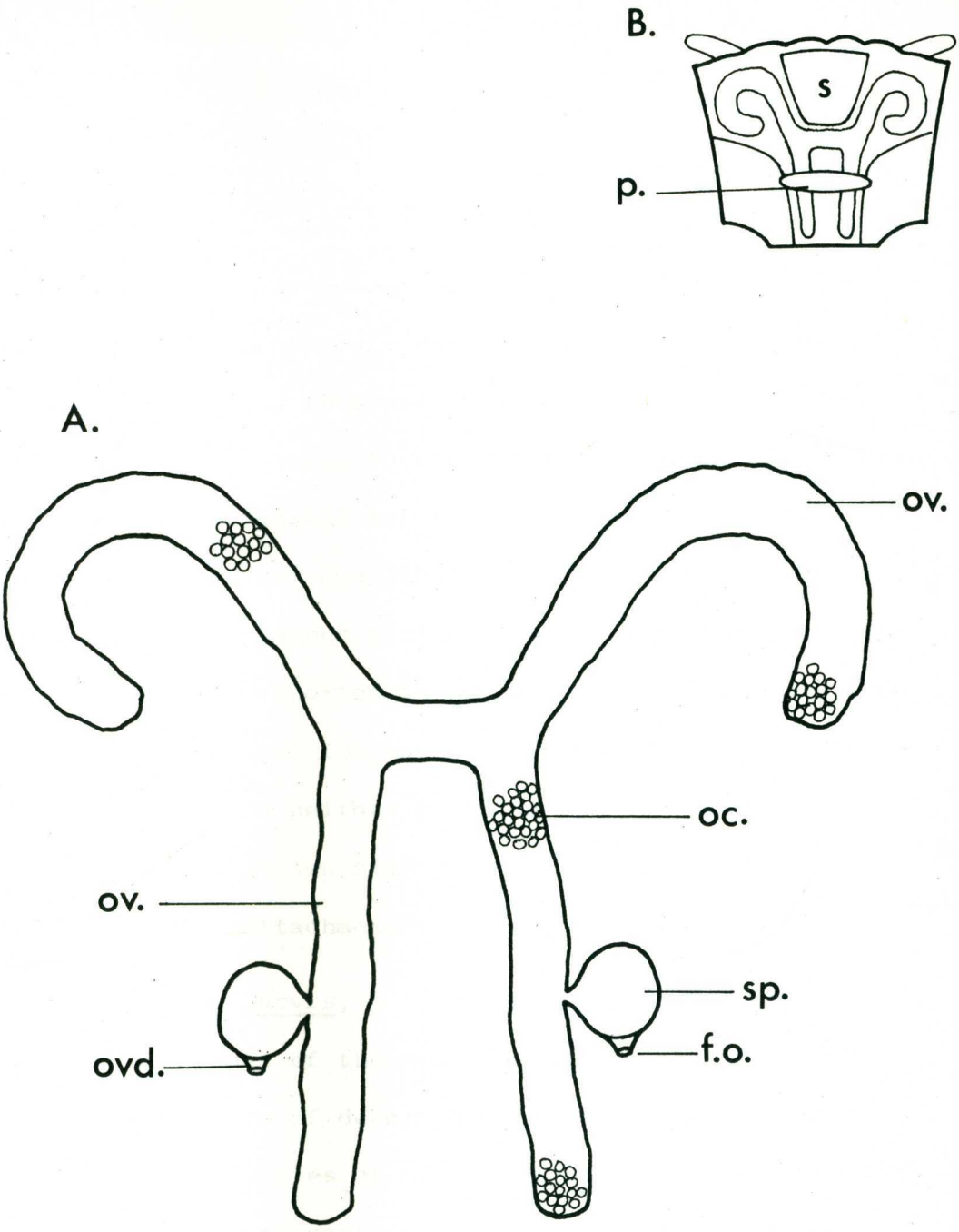
4.3 RESULTS

4.31 Anatomy and External Appearance of the Ovary.

The ovaries are paired, symmetrical organs situated in the cephalothorax below the dermis. Their general shape resembles the letter X (Fig. 4-1). From the antero-lateral portions in the front gill region of the head and thorax, where they lie above the digestive gland, they extend downwards past the sides of the fore-gut. Here they are connected by a strand of gonadial tissue which forms a bridge over the mid-gut. From this transverse connection the ovaries continue backwards as two strips of tissue above the hind-gut and beneath the pericardium to the posterior end of the thorax. There is no fusion of the two ovaries at the posterior end of the thorax in any of the four species examined, as was described in mature specimens of Cancer pagurus by Pearson (1908). Each of the posterior branches is connected on its outer side at the level of the pericardium to a sac-like spermatheca. A short oviduct leads from each spermatheca and opens to the exterior by means of the vulva on the sternum of the sixth thoracic somite.

FIG. 4-1

Female reproductive system of a crab. A, generalised diagram. B, position of ovaries in the crab. ov., ovary; ovd., oviduct; oc., oocyte; f.o., female genital opening; sp., spermatheca; s., stomach; p., pericardium.


B.
s
p.
A.
ov.
oc.
ov.
sp.
ovd.
f.o.

The size and appearance of the ovaries varied considerably according to the degree of maturity of the crab. In all four species the most immature ovaries were narrow white strips of tissue inside which no oocytes were discernible. As they matured the ovaries assumed the colour of the developing oocytes within them and changed through pale yellow, to orange and then to dark brown. By this stage the oocytes ranged up to 400 µm in diameter and were clearly visible to the naked eye beneath the transparent epithelial layer around the ovary. The ovary now took up most of the available space in the cephalothorax. Similar colour changes in the external appearance of ovaries of crabs have been reported in Cancer pagurus (Pearson, 1908; Eurenius, 1973) and the tanner crab Chionoecetes opilio (Kon and Honma, 1970). In neither of these species, however, was there any report of a brown stage in the development of the oocytes prior to their attachment to the ventral surface of the abdomen.

In P. laevis, S. erythrodactyla and A. tridentata the changes of colour of the ovaries were fairly uniform, reflecting the uniform state of development of the outermost oocytes in the ovary. Where oocytes of different colours were present they were usually in two successive stages (i.e. oocytes of only two colours were present). In contrast, the ovaries of H. cordiformis often contained oocytes ranging through all stages of development, spread randomly throughout the ovaries. This contrasts with Chionoecetes opilio (Kon and Honma, 1970) in which all the oocytes on the outside of the ovary were reported to be uniform in colour.

Oocytes attached to the exterior abdominal appendages of all species examined here ranged in diameter from 300 to 500 µm.

In some cases their external appearance was identical to the brown stage found within the cephalo-thorax. In others, the form of the zoea larva was clearly visible within the transparent epithelial membrane, and the large eyespots and beating heart could be seen.

4.32 Oogenesis

The structure of the ovaries and general features of oogenesis of S. erythrodactyla, P. laevis and H. cordiformis were very similar. Transverse sections revealed that the ovary is enclosed in a layer of connective tissue. Portions of tissue extend at frequent intervals into the interior of the ovary forming trabeculae which divide the ovary into separate compartments. This is particularly evident in ovaries where large numbers of small immature oocytes are developing inside large compartments that appear to have held mature oocytes from the previous season. A median canal was observed in most specimens and this appeared to have canals branching from it (Figs. 4-2, 4-3, 4-4).

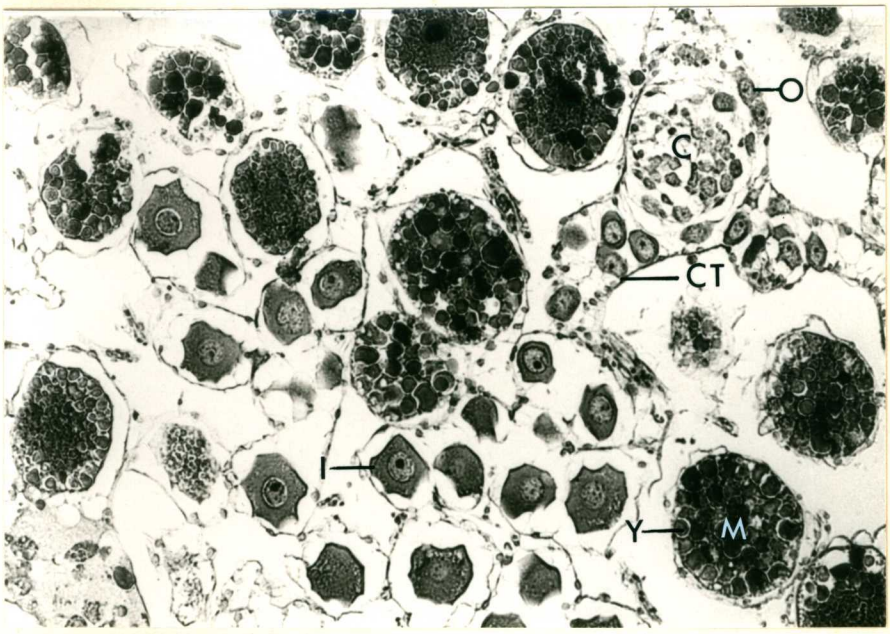
Oogonia were confined to the median canal of the ovary. They appeared at a magnification of x 100 as small circular cells, with a clear nucleus surrounded by a narrow band of brown staining material, which developed into the cytoplasm in the immature oocyte. (Figs. 4-2, 4-3, 4-4). There were no discernible structures in the nucleus. The maximum diameter of oogonia was 10 µm.

As the developing oocyte enlarged, cytoplasm expanded around the nucleus. The cytoplasm was homogeneous in appearance and stained brown. The nucleus was surrounded by a distinct nuclear membrane and was clear except for a dark staining nucleolus. In

FIG. 4-2

Transverse sections of ovary of Sesarma erythrodactyla (x 100). A, June. B, September. C, March. (O, oogonium; I, immature oocyte; M, mature oocyte; C, median canal; CT, connective tissue; Y, yolk droplet).

A



B

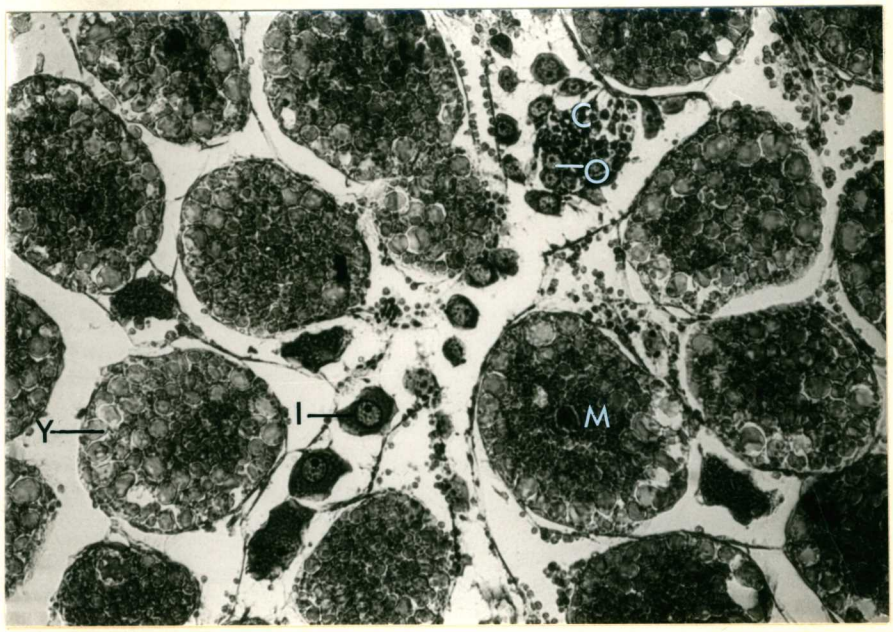


FIG. 4-2 (cont.)

C

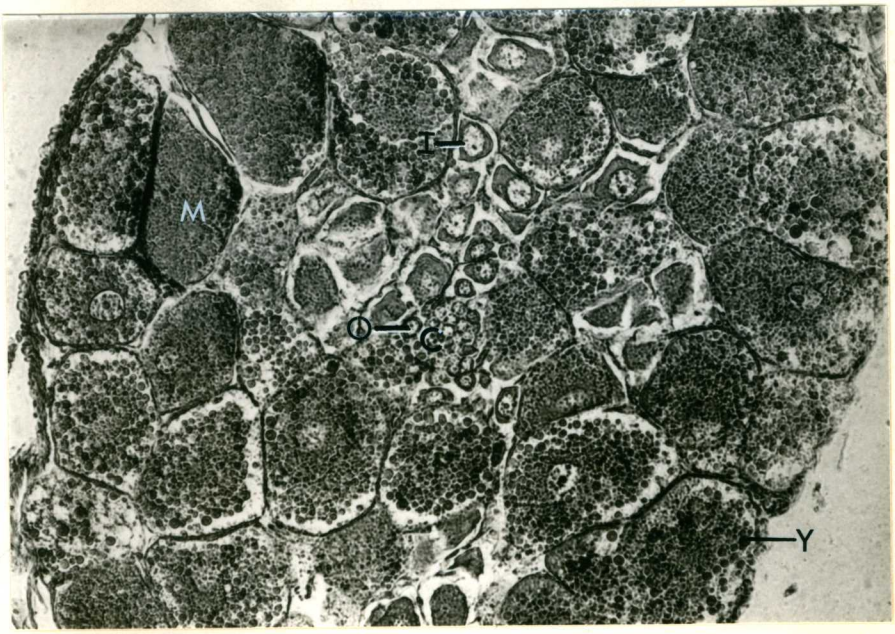


FIG. 4-3

Transverse sections of ovary of Paragrapsus laevis (x 100).

A, January. B, June. C, August. D, September, E, October.

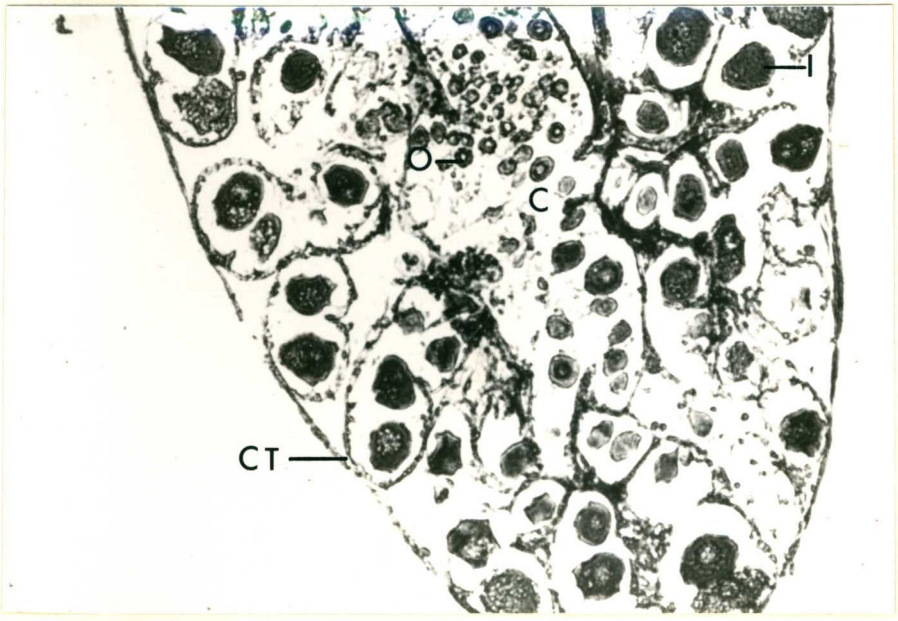
F, December.

(O, oogonium; I, immature oocyte; M, mature oocyte;

D, degenerating oocyte; C, median canal; CT, connective

tissue; Y, yolk droplet).

A



B

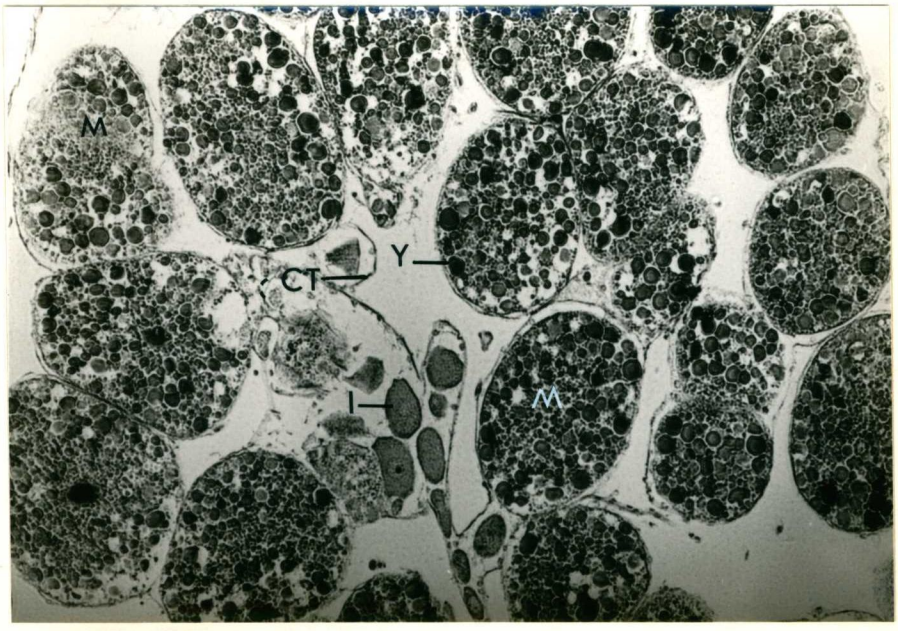
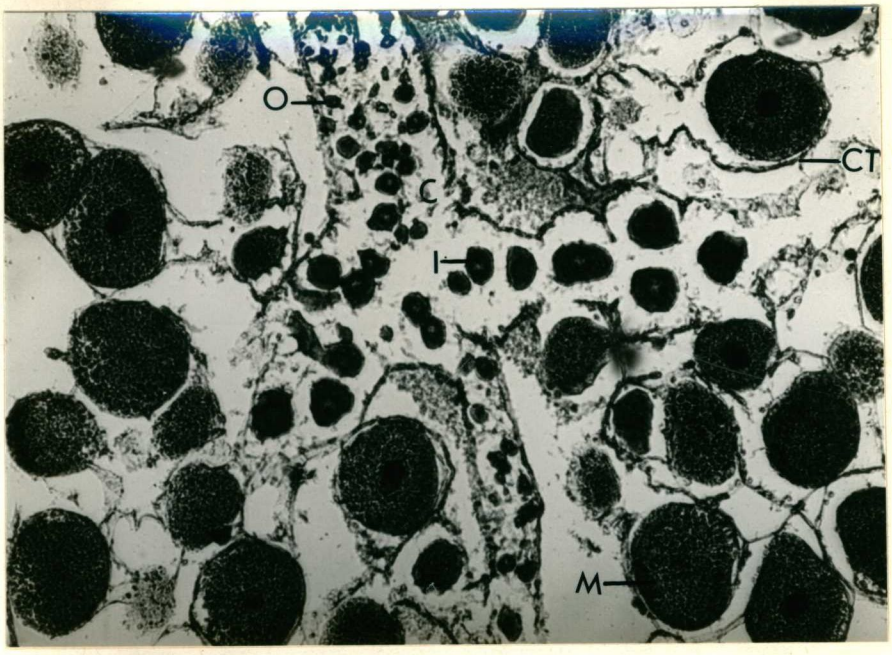


FIG. 4-3 (cont.)

C



D

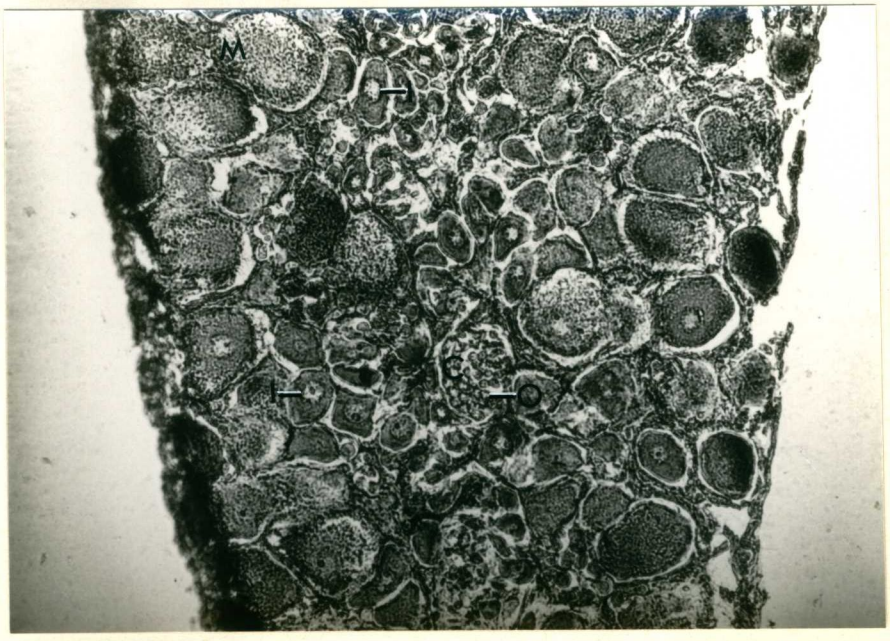
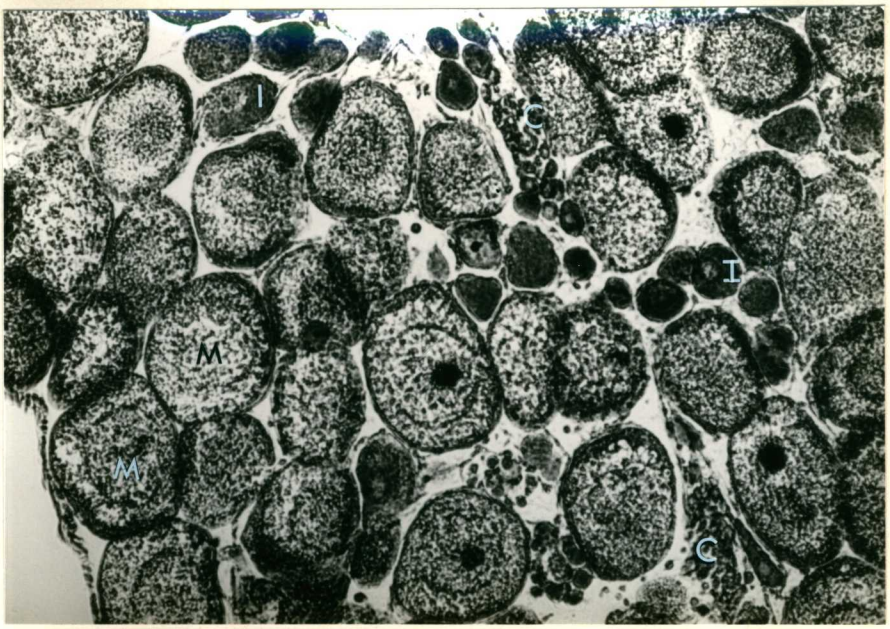


FIG. 4-3 (cont.)

E



F

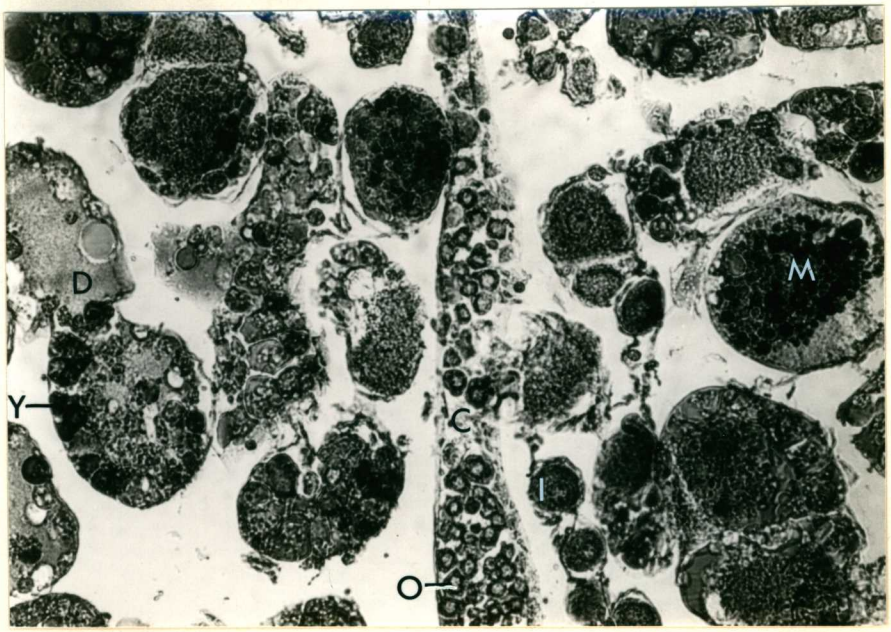
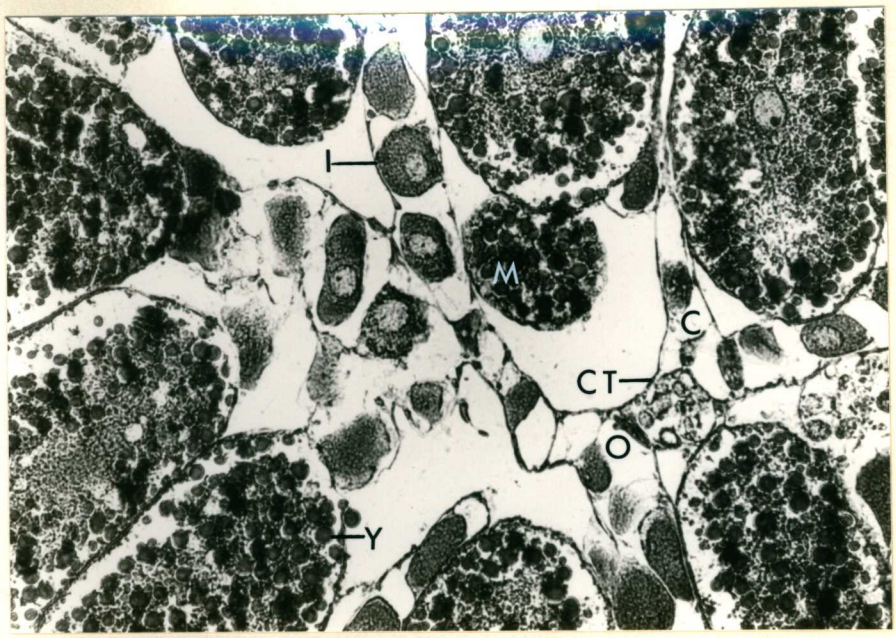


FIG. 4-4

Transverse sections of ovary of Heloecius cordiformis (x 100). A, February, B, C, October. D, December. (O, oogonium; I, immature oocyte; M, mature oocyte; D, degenerating oocyte; C, median canal; CT, connective tissue; Y, yolk droplet).

A



B

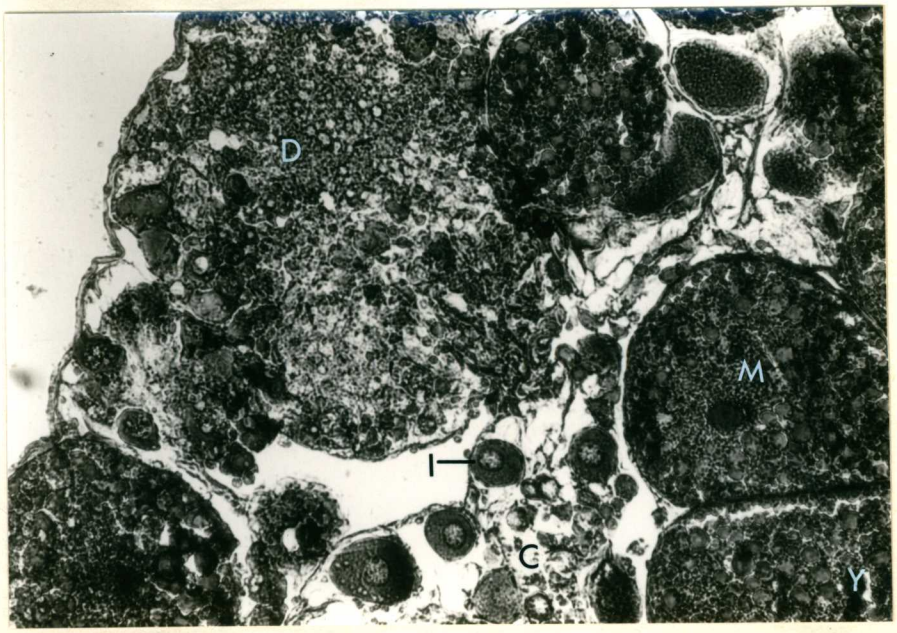
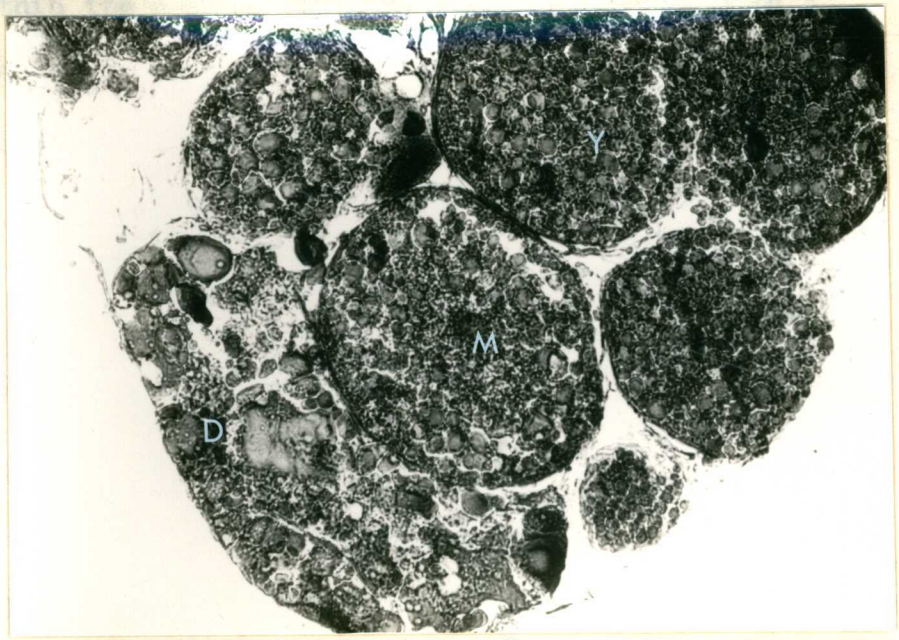
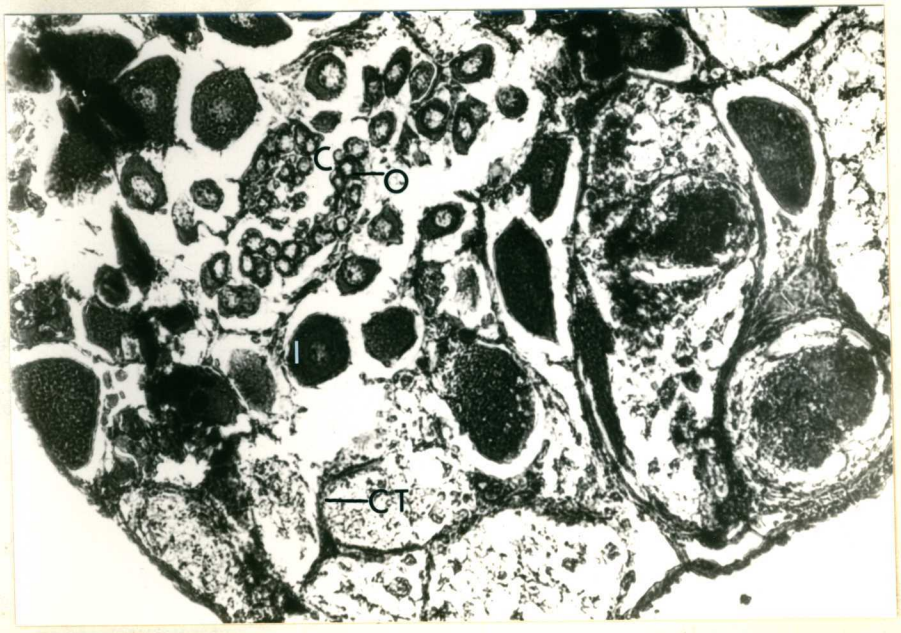


FIG. 4-4 (cont.)

C



D



P. laevis and H. cordiformis some immature oocytes had two nucleoli within the nucleus, while the majority had only a single nucleolus. Nuclei with two nucleoli were not found in S. erythrodactyla. Oocytes at this stage of development ranged from 10 μm up to a maximum diameter of 70 μm. The smallest of them were generally located in the median canal of the ovary and their size increased as they moved outward along the branch canals (Figs. 4-2, 4-3, 4-4).

Follicle cells surrounded the growing oocytes. The presence of follicle cells in crab ovaries has also been reported in Cancer pagurus (Eurenius, 1973) and in the tanner crab Chionoecetes opilio (Kon and Honma, 1970a) and in other crustacea such as the lobster Homarus (Kessel, 1968).

Further enlargement of the oocytes was accompanied by the cytoplasm becoming more diffuse and granular in appearance and the formation of spherical droplets in the cytoplasm (Figs. 4-2, 4-3, 4-4). Some of these droplets stained grey indicating a high concentration of protein. Others stained brown and probably consisted of lipid. The beginning of this stage signalled the onset of vitellogenesis. Thus, yolk in the eggs of these crabs consists of separate lipid and protein droplets. This has been described in a similar way, and in oocytes of the same size, in Cancer pagurus (Eurenius, 1973) and in Chionoecetes opilio (Kon and Honma, 1970a). Subsequent growth in size of the oocytes was accompanied by enlargement of the droplets until they reached a maximum diameter of 10-20 μm and occupied most of the space in the oocyte. Coincident with the formation of droplets within the oocytes the nuclear

membrane became indistinct and in many cases the brown or grey staining nucleolus was the only recognisable part of the nucleus visible.

Vitellogenic oocytes were generally most numerous in the periphery of the ovary, with the smallest towards the centre. In mature ovaries, however, they occupied most of the available space and compartments within the ovary were often indistinct.

The ovaries of P. laevis showed some variation from the above pattern. In many of the ovaries examined droplets appeared in the cytoplasm of the oocytes once they had grown larger than about 70 μm diameter. Some oocytes as small as 70 μm were packed with large droplets. In P. laevis, however, the oocytes in some specimens had enlarged without droplets forming. Some ovaries were packed with oocytes up to 160 μm in diameter, in which the cytoplasm had become diffuse and granular, but in which no droplets were present (Fig. 4-3). The appearance of the nucleus in such oocytes varied. In some it was similar to those in vitellogenic oocytes, i.e. the nuclear membrane was indistinct and only a large grey, or occasionally brown, staining nucleolus was visible. In other oocytes, the nuclear membrane was easily visible and a small nucleolus was often present. Kon and Honma (1970a) reported that the ovaries of many female Chionoecetes opilio had not accumulated large yolk granules even though the diameter of the oocytes reached 200-250 μm. The significance of this phenomenon is not clear.

For the purpose of quantifying the degree of maturity of crabs in the population, oocytes were assigned to two groups: mature and immature. Mature oocytes included all those in which

TABLE 4-1

Analysis of variance of multiple regression on percentage of mature oocytes of Sesarma erythrodactyla during the study.

Source of variation	Sum of squares	Degrees of freedom	Mean Square	F-ratio
Regression on sin x + cos x	3668.67	2	1834.33	8.82**
Deviations from regression	2078.92	10	207.89	
Total	5747.59	12		

the presence of large droplets indicated that vitellogensis had taken place. For P. laevis, those oocytes with dispersed and granular cytoplasm were defined as mature, though no large yolk droplets were visible. All other oocytes were regarded as immature.

4.33 Seasonal Changes in the Ovary

(i) Sesarma erythrodactyla

Variations in the mean numbers of mature and immature oocytes, the mean percentage of mature oocytes and in the mean diameter of mature oocytes of S. erythrodactyla are shown in Fig. 4-5. Multiple regression analysis on the percentage of mature oocytes was used to fit the results to the curve $y = a + b_1 \sin x + b_2 \cos x$ in which y = mean number of mature oocytes per month

x = the month expressed as an angle between 0^o and 360^o,

a = intercept, and

b_1 and b_2 = regression coefficients.

a, b_1 and b_2 were estimated by multiple regression on sin x + cos x. The result of this multiple regression was significant (Table 4-1) and the regression curve is shown in Fig. 4-5.

The mean percentage of mature oocytes increased steadily from May, 1974, to a peak in November, 1974. It then declined to minimal values from April to June, 1975, before beginning to increase again. Variation in the mean numbers of mature oocytes was consistent with this trend. There were more mature oocytes

FIG. 4-5

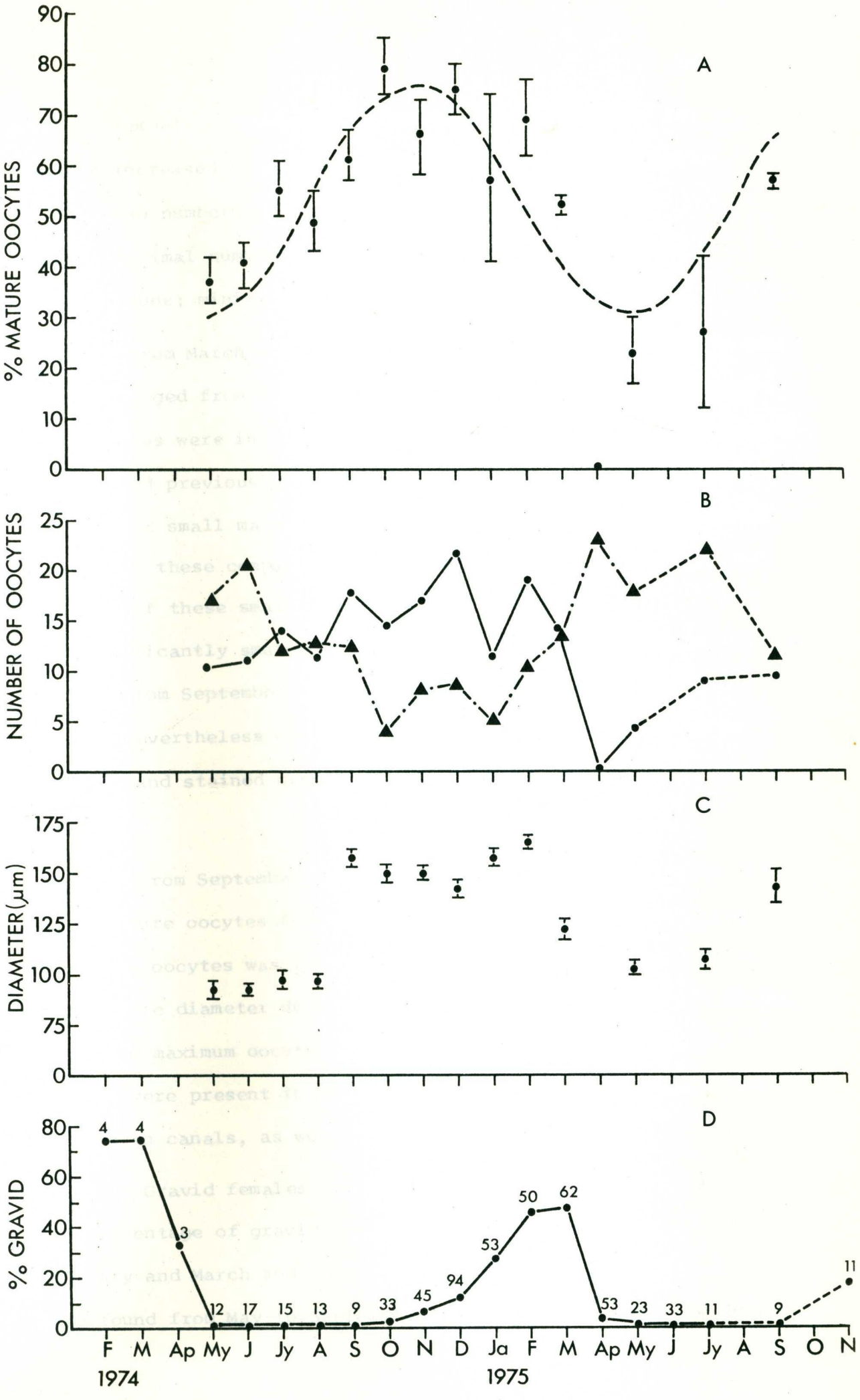
Reproductive cycle of Sesarma erythrodactyla.

A. Variation in mean percentage (± 95% confidence limit) of mature oocytes. Regression curve is shown.

B. Variation in mean numbers of mature (• ——— •) and immature (▲ —— • —— ▲) oocytes.

C. Variation in mean diameter (± 95% confidence limit) of mature oocytes.

D. Occurrence of gravid females. Numbers above points on the graph indicate total numbers of females caught during each month.


A
% MATURE OOCYTES
90
80
70
60
50
40
30
20
10
0
B
NUMBER OF OOCYTES
25
20
15
10
5
0
C
DIAMETER(μm)
175
150
125
100
75
0
D
% GRAVID
80
60
40
20
0
4
4
3
12
17
15
13
9
33
45
94
53
50
62
53
23
33
11
9
11
F
M
Ap
My
J
Jy
A
S
O
N
D
Ja
F
M
Ap
My
J
Jy
A
S
O
N
1974
1975

from September to February and low numbers in April. The numbers increased steadily from April (Fig. 4-5). Variation in the mean numbers of immature oocytes showed the opposite trend. Maximal numbers of immature oocytes were present from April to June; minimal numbers from October to January (Fig. 4-5).

From March to August, when the mean percentage of mature oocytes ranged from 0-55%, there were empty spaces in the ovary. These spaces were in compartments of the ovary which were apparently occupied previously by large mature oocytes. Some immature oocytes, or small mature oocytes, or a mixture of the two, were present in these compartments, but did not fill them. The mean diameter of these small mature oocytes was about 90 µm, which was significantly smaller than the mean diameter of mature oocytes present from September to February (Fig. 4-5). These smaller oocytes nevertheless contained granules that were up to 10 µm diameter and stained grey or brown and were considered to be mature.

From September to February the ovaries were packed with large mature oocytes (Fig. 4-5). The maximum mean percentage of mature oocytes was 79%. There was little variation in the mean oocyte diameter during this period; it varied around 150 µm, while the maximum oocyte diameter reached 300 µm. Immature oocytes were present in minimal numbers and were restricted to the median canals, as were oogonia.

Gravid females first appeared in October (Fig. 4-5). The percentage of gravid females then increased to a maximum in February and March and then rapidly declined. No gravid females were found from May to September. Oocytes thus appear to develop

TABLE 4-2

Analysis of variance of multiple regression on percentage of mature oocytes of *Paragrapsus laevis* during the study.

Source of variation	Sum of squares	Degrees of freedom	Mean square	F-ratio
Regression on sin x + cos x	6958.65	2	3479.33	11.27**
Deviations from regression	3086.54	10	308.65	
Total	10045.19	12		

soon after spawning and undergo vitellogenesis and increase in size from May to October. They are then stored for some time before spawning when they become attached to the ventral surface of the abdomen.

There was little evidence of degeneration or resorption of mature oocytes which remained in the ovary after spawning. Large mature oocytes disappeared from the ovary after March (Fig. 4-5).

(ii) Paragrapsus laevis

Variations in the mean numbers of mature and immature oocytes, the mean percentages of mature oocytes and the mean diameter of mature oocytes of P. laevis during the period of sampling are shown in Fig. 4-6. Multiple regression analysis on the mean percentage of mature oocytes was used as for S. erythrodactyla, to detect annual trends by fitting the results to the curve $y = a + b_1 \sin x + b_2 \cos x$. (see page 104). The regression analysis was significant (Table 4-2). The regression is shown in Fig. 4-6.

The mean percentage of mature oocytes was at a peak in April, 1974. The percentage of mature oocytes continued at high levels (80-90%) throughout May and June, 1974. Most of the ovaries examined were full of mature oocytes up to a maximum of 300 μm in diameter. The few immature oocytes present in the ovaries at this time were restricted to the median canal. Some ovaries appeared to be in an irregular state and had many empty compartments. Mature oocytes had probably recently passed out of these

FIG. 4-6

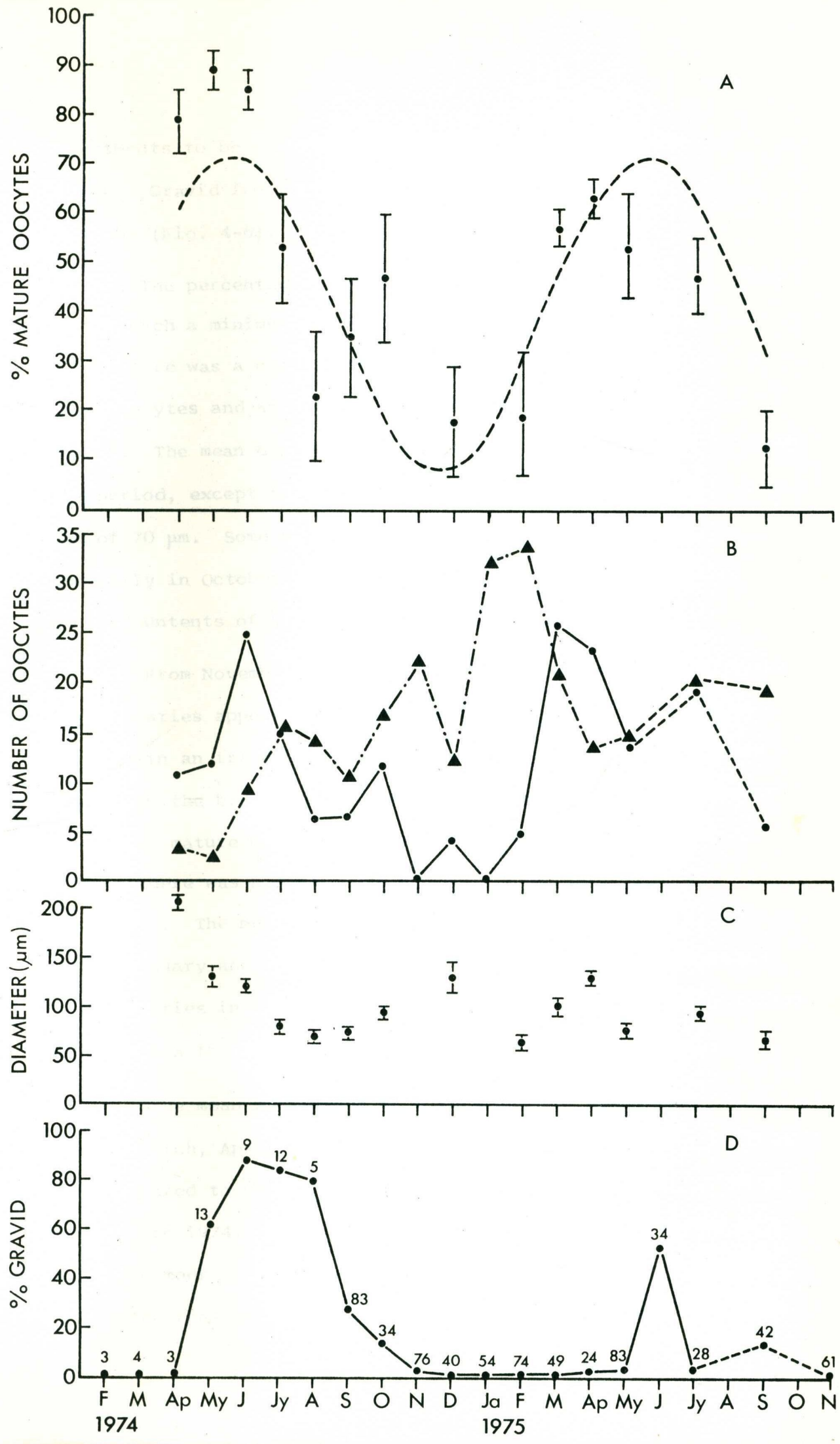
Reproductive cycle of Paragrapsus laevis.

A. Variation in mean percentage (± 95% confidence limit) of mature oocytes. Regression curve is shown.

B. Variation in mean numbers of mature (• ——— •) and immature (▲ —— • —— ▲) oocytes.

C. Variation in mean diameter (± 95% confidence limit) of mature oocytes.

D. Occurrence of gravid females. Numbers above points on the graph indicate total numbers of females caught during each month.


A
% MATURE OOCYTES
100
90
80
70
60
50
40
30
20
10
0
B
NUMBER OF OOCYTES
35
30
25
20
15
10
5
0
C
DIAMETER (μm)
200
150
100
50
0
D
% GRAVID
100
80
60
40
20
0
3
4
3
13
9
12
5
83
34
76
40
54
74
49
24
83
34
28
42
61
F M Ap My J Jy A S O N D Ja F M Ap My J Jy A S O N
1974
1975

compartments to be attached to the ventral surface of the abdomen. Gravid females were present in the population at this time (Fig. 4-6).

The percentage of mature oocytes decreased steadily from May to reach a minimum in November and December. During this period there was a corresponding decrease in the mean number of mature oocytes and an increase in the mean number of immature oocytes. The mean diameter of mature oocytes also declined during this period, except in October and December, to a mean minimum size of 70 μm. Some of the larger mature oocytes present, especially in October and December, seemed to be degenerating and the contents of some ovaries were irregular.

From November to January the only mature oocytes present in the ovaries appeared to be degenerating. Many ovaries also appeared in an irregular state. There were many small immature oocytes in the branch canals or filling some of the compartments vacated by mature oocytes. Because of the small size of these oocytes there was a great deal of empty space in the ovary (Fig. 4-3). The mean number of immature oocytes was at a maximum in January and February. Small mature oocytes were present in the ovaries in February. The median canal was generally filled with oogonia throughout this period.

The mean percentage of mature oocytes again rose to a peak in March, April and May, 1975, although it varied from 50 to 65%, compared to values from 80 to 90% during the same period of the year in 1974. This decrease was caused by the presence of a greater number of immature oocytes in the ovary in 1975 than in 1974. The reasons for this are not clear. The condition of the

TABLE 4-3

Analysis of variance of multiple regression on percentage of mature oocytes of Heloecius cordiformis during the study.

Source of variation	Sum of squares	Degrees of freedom	Mean square	F-ratio
Regression on sin x + cos x	1373.93	2	686.96	6.91*
Deviations from regression	994.43	10	99.44	
Total	2368.36	12		

ovaries was much the same as during the corresponding months in 1974, the presence of large numbers of mature oocytes being the dominant feature.

Gravid females were found from May to October in both 1974 and 1975. The first gravid females appeared in the population at a time when the percentage of mature oocytes was at a peak. There was no evidence of storage of mature oocytes as indicated in S. erythrodactyla, where the percentage of mature oocytes rose to a peak about three months before the maximum numbers of gravid females occurred. No gravid females were found from November to May.

(iii) Heloecius cordiformis.

Seasonal variations in the mean numbers of mature and immature oocytes, the mean percentages of mature oocytes and the mean diameter of mature oocytes of H. cordiformis are shown in Fig. 4-7. Multiple regression analysis on the mean percentage of mature oocytes was used as for S. erythrodactyla (see page 104). The regression analysis was significant (Table 4-3). The regression is shown in Fig. 4-7.

The mean percentage of mature oocytes reached a peak during the period from March to June, 1974, and began to decline in July and August, 1974. Most ovaries during these periods contained large mature oocytes. As with the species described previously, these were concentrated towards the outside of the ovary, except when the ovary was completely filled by them (Fig. 4-7). The maximum observed size of mature oocytes was 300 μm, while the mean size ranged from 130 μm to 200 μm. Many of the other ovaries examined during this period contained some large, empty, membrane-

FIG. 4-7

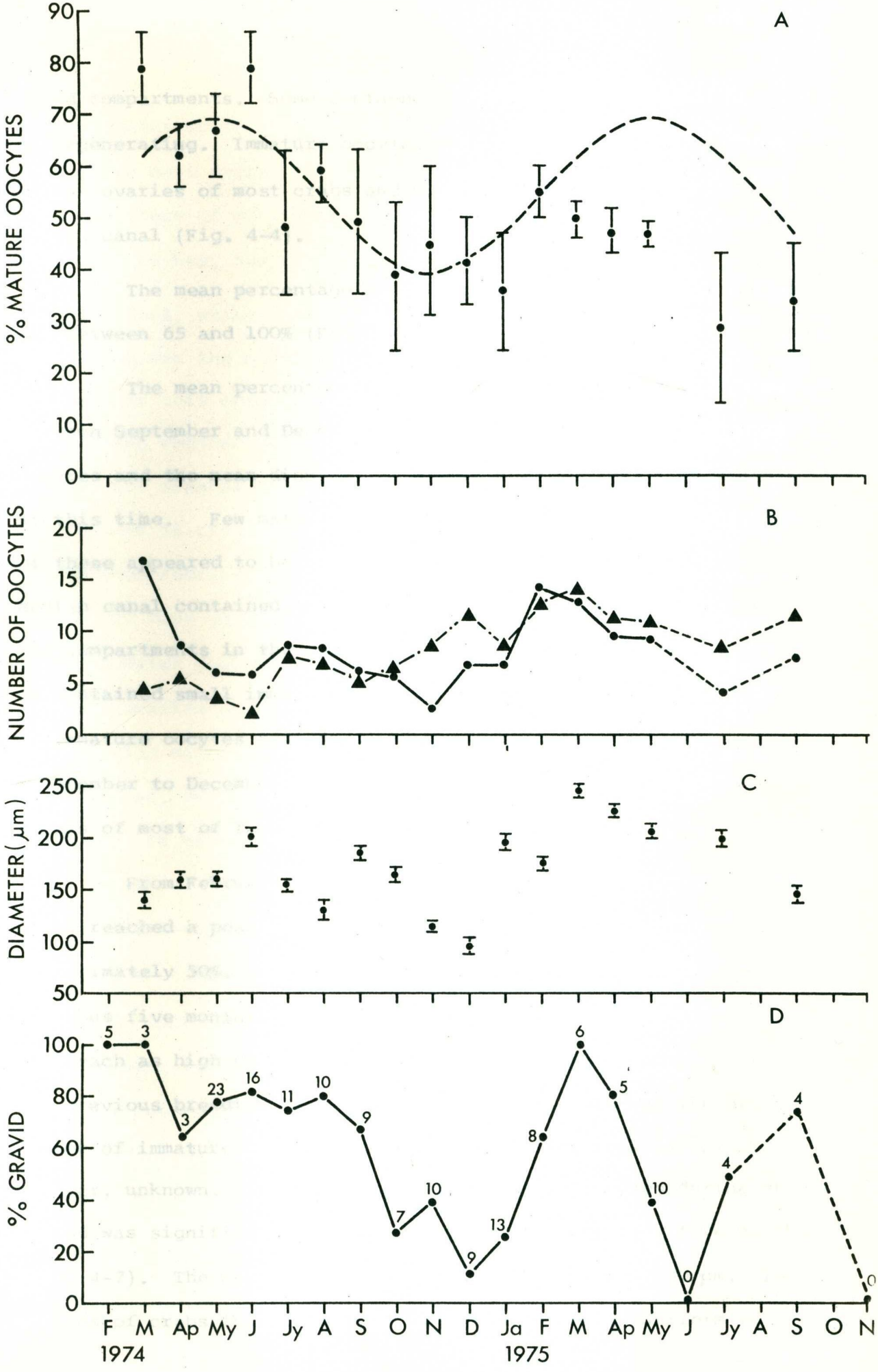
Reproductive cycle of Heloecius cordiformis.

A. Variation in mean percentage (± 95% confidence limit) of mature oocytes. Regression curve is shown.

B. Variation in mean numbers of mature (• ——— •) and immature (▲ —• — ▲) oocytes.

C. Variation in mean diameter (± 95% confidence limit) of mature oocytes.

D. Occurrence of gravid females. Numbers above points on the graph indicate total numbers of females caught during each month.


A
% MATURE OOCYTES
90
80
70
60
50
40
30
20
10
0
B
NUMBER OF OOCYTES
20
15
10
5
0
C
DIAMETER (μm)
250
200
150
100
50
D
% GRAVID
100
80
60
40
20
0
5
3
3
23
16
11
10
9
7
10
9
13
8
6
5
10
0
4
4
0
F
M
Ap
My
J
Jy
A
S
O
N
D
Ja
F
M
Ap
My
J
Jy
A
S
O
N
1974
1975

bound compartments. Some contained oocytes which appeared to be degenerating. Immature oocytes were present in small numbers in the ovaries of most crabs and most contained oogonia in the median canal (Fig. 4-4).

The mean percentage of gravid females during this period was between 65 and 100% (Fig. 4-7).

The mean percentage of mature oocytes reached a minimum between September and December, 1974. The mean number of mature oocytes and the mean diameter of mature oocytes were also minimal at this time. Few mature oocytes were present, and the majority of these appeared to be breaking down. In some ovaries, the median canal contained the remains of mature oocytes. Most of the compartments in the periphery of the ovaries were either empty, or contained small immature oocytes (Fig. 4-4). The mean number of immature oocytes rose steadily throughout this period (September to December). Oogonia were present in the median canals of most of the ovaries examined.

From February to May, 1975, the number of mature oocytes again reached a peak. The mean percentage of mature oocytes was approximately 50%. Although this was greater than during the previous five months, the mean percentage of mature oocytes did not reach as high values (i.e. 80%) as in the same months during the previous breeding season. The reason for this was the greater number of immature oocytes present in 1975, for reasons which are, however, unknown. The mean diameter of mature oocytes during this period was significantly greater than for the previous five months (Fig. 4-7). The maximum diameter of the oocytes was 350 μm. The ovaries of crabs throughout this period were fairly uniform in

appearance. Most were packed with mature oocytes containing yolk droplets up to 20 μm in diameter. Immature oocytes were present in most ovaries, as well as oogonia in the median canal. The percentage of gravid females also peaked during this period (February to May, see Fig. 4-7).

Thus, while the numbers of gravid H. cordiformis were fewer than for the other two species, due to the small number of crabs of this species caught in traps and the inability of determining whether or not crabs were gravid in the photographic census, the seasonal variations in the reproductive condition of the females is clear. The percentage of mature oocytes rises to a peak from February to June, when the ovaries are full of mature oocytes or have just released mature oocytes. The percentage of mature oocytes declines to a minimum from September to December, when the ovaries contain large numbers of immature oocytes or degenerating mature oocytes. Gravid females are present throughout the year, but their numbers vary with variations in the percentage of mature oocytes (see Fig. 4-7).

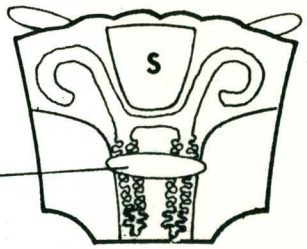
4.34 Anatomy and External Appearance of the Male Reproductive System

The testes are paired symmetrical organs situated in the antero-lateral region of the cephalothorax, immediately below the dermis and above the digestive gland (Fig. 4-8). Each testis is made up of a single seminiferous tubule, ranging in diameter from 0.1 to 0.5 mm. The testis is very long because it is tightly coiled. It traverses a path beginning in the area of the front gill, ascends towards the rear of the eyestalks, passes

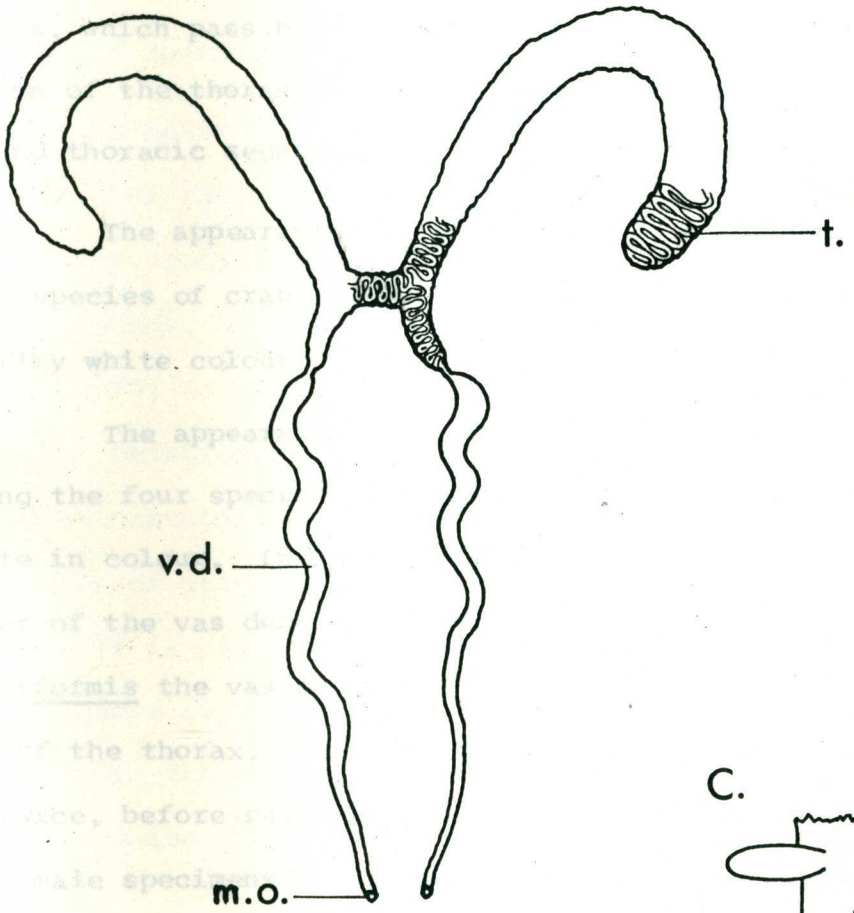
FIG. 4-8

Male reproductive system of a crab. A, generalised diagram. B, position of male reproductive system in a crab. C, section of vas deferens of Sesarma erythrodactyla showing diverticula. t., testis; v.d., vas deferens, m.o., male genital opening; d., diverticulum; s., stomach; p., pericardium.

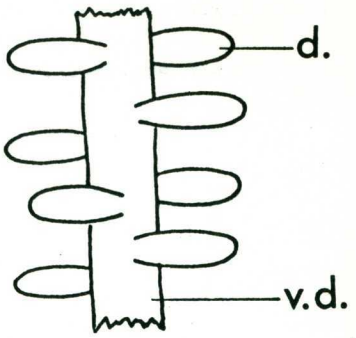
B.



A.



C.



the side of the stomach and then meets the vas deferens near the cardiac fore-gut. The two testes are joined by a bridge of gonadial tissue which passes behind the pyloric fore-gut. The vasa deferentia are long tubes, much thicker than the testis, which pass backwards from the testis to the posterior region of the thorax, where each opens to the exterior from the second thoracic segment.

The appearance of the testes was very similar in all four species of crab. The testes varied from transparent to a milky white colour.

The appearance and structure of the vas deferens varied among the four species of crabs. In all species it was milky white in colour. In H. cordiformis and A. tridentata the diameter of the vas deferens varied from 0.3 to 1.2 mm. In H. cordiformis the vas deferens passed straight back to the posterior end of the thorax. In many crabs it doubled back on itself once or twice, before reaching the posterior end of the thorax. In most male specimens of A. tridentata, the vas deferens was a straight tube. Only in a few did it double back on itself. In two specimens of A. tridentata there were lobular diverticula from the posterior end of the vas deferens.

The main tube of the vas deferens in both of the grapsids varied in diameter from 0.5 to 1.5 mm. In P. laevis the vas deferens passed straight backwards with some small bends in its path. In some P. laevis lobular diverticula were present at the posterior end of each vas deferens. These were similar to those seen in A. tridentata. In S. erythrodactyla the entire length of

the vas deferens had diverticula extending horizontally from both sides of the main tube. These were present in all S. erythrodactyla examined throughout the year and were up to 2 mm long. The significance of these diverticula is unclear, but they probably increase the volume of the vas deferens for the storage of spermatocytes.

No consistent seasonal trends in the appearance or structure of the male reproductive systems of any of the four species of crabs could be detected from external examination of the gonads. A similar conclusion was reached by Kon and Honma (1970) in their study of the male tanner crab, Chionoecetes opilio. Detailed monthly histological examination of the testes would be necessary to determine changes in the reproductive condition of male crabs. This was not possible in the present study. It is reasonable to suggest, however, that the male reproductive cycle would match that of the females, so that peak activity in the testes would occur before the appearance of gravid females.

4.4 DISCUSSION

The basic structures of the female reproductive systems and the patterns of oogenesis were very similar in the three species of crabs examined. (These were compared on pages 99-104). The major differences are in the seasonal timing of the reproductive cycles. Sesarma erythrodactyla have the greatest percentage of mature oocytes in Spring and early Summer and appear to store mature oocytes until late Summer and early Autumn when gravid crabs are most abundant. Heloecius cordiformis and

Paragrapsus laevis have the greatest percentage of mature oocytes in Autumn and Winter. The greatest percentage of gravid crabs of these two species also occur in Autumn and Winter. There is no evidence of storage of oocytes in either of these two species.

Gravid H. cordiformis were present throughout the year. This contrasts with the situation in Tasmania, the southern limit of the distribution of this species. Griffin (1971) found that H. cordiformis were gravid in November, December and January, but not gravid from April to September. The more restricted breeding season found in Tasmania is probably related to the greater seasonal fluctuations in temperature there. Goodbody, 1961, and Warner, 1967, suggested that many animals living in the Tropics breed throughout the year because seasonal changes in temperature are not sufficient to have any noticeable effect on breeding cycles.

Green and Anderson (1973) found numerous gravid S. erythrodactyla in February and March at Port Hacking, New South Wales, about 80 km south of the study site at Patonga. No gravid females were found from April to September. This is consistent with the results found in the present study. Green and Anderson (1973) also found two gravid P. laevis (= Chasmagnathus laevis; Campbell and Griffin, 1966) in February, but none throughout the rest of the sampling period, which was from February to September. These results implied that P. laevis have a short breeding season in the late Spring and Summer (from October to February). This is the exact opposite to what was found in the present study. The reason

for this discrepancy is unknown.

Griffin (1971) found gravid P. laevis in Tasmania in October, which is consistent with the results of the present study. Gravid P. laevis were not found by Griffin in other months due to the small samples collected.

SECTION 5 : GENERAL DISCUSSION.

The mangrove study site at Patonga differs markedly from other mangrove areas in which the distribution of fauna has been investigated. It is near the southern limit of the distribution of mangroves and only two species, *Avicennia marina* and *Aegiceras corniculatum*, are present. Most previous studies of mangrove fauna have been conducted in the Tropics, where more species of mangroves are present and the general structure of swamps is more complex (see page 15).

Another basic difference is the composition of the substratum. The mean percentages of coarse sand and fine particles (fine sand, silt and clay) in the study area are about 90% and 5%, respectively. In contrast, the mean percentages of coarse sand and fine particles from two other mangrove swamps on which studies of fauna have been made, are about 15% and 82%, respectively, at Ao Nam-Bor, Thailand (Frith *et al.*, 1976) and about 1% and 99%, respectively, at Port Swettenham, Malaysia (Sasekumar, 1974). Warner (1969) studied crabs in a mangrove swamp in Jamaica. Although the composition of the substratum was not analysed, Warner described it as ranging from firm clean peat lower on the shore to soft muddy peat higher on the shore. The extremely high percentage of coarse sand in the substratum at Patonga influences both the moisture content and amount of organic matter in the substratum. The mean moisture content of the soil at Patonga was about 19%, compared with 36% at Ao Nam-Bor and 42% at Port Swettenham. (As the latter two figures were calculated as percentage of wet weight of soil, and the former as percentage of dry weight of soil, the differences are

actually greater.) Newell (1970) showed that the concentration of organic matter in intertidal deposits increased as the deposit became finer. The mean organic content of the soil over all zones at Patonga was about 3%, compared to about 8% at Ao Nam-Bor and 4% at Port Swettenham.

Despite these differences, the fauna in the mangrove swamp at Patonga shows many similarities with the fauna in mangrove swamps in other parts of the world.

The crabs present at Patonga show vertical zonation on the shore which is related to the zonation of the mangrove trees (Fig. 3-15). Zone I is lowest on the shore. Pneumatophores of A. marina and oysters are present in Zone I in large numbers, but there are no mangrove trees. The soil in this zone contains significantly more fine particles (clay, silt, fine sand) and has the highest moisture content of all zones. The two species of crabs were found exclusively in Zone I: the xanthid, Pilumnopeus serratifrons, which lives beneath oysters and pieces of timber, and the small grapsid, Ilyograpsus paludicola, which lives in the soil among the oysters. Two ocypodids were also present in their greatest numbers on the shore, Helocius cordiformis and Australoplax tridentata. Both species live in burrows in the soil. Two grapsids, Paragrapsus laevis and Sesarma erythrodactyla were also present.

A. marina trees grow in Zone II; pneumatophores are present in large numbers and small numbers of oysters lie on the surface of the ground. P. laevis was found here in greatest numbers; S. erythrodactyla, H. cordiformis, A. tridentata and Helice leachii were also present.

Zone III is the widest zone on the shore and both mangrove trees, A. marina and A. corniculatum, grow there. Pneumatophores are present in smaller numbers than in Zones I and II, oysters are absent, and the moisture content of the soil is the lowest of the four zones. Zone III can be compared to the "transition" zone described by Warner (1969). No species of crab was found exclusively there or in its greatest numbers there. The crabs, P. laevis, S. erythrodactyla, H. cordiformis and H. leachii were all present there.

Zone IV is the highest zone on the shore and is characterised by large numbers of A. corniculatum and smaller numbers of A. marina growing there. The smallest numbers of pneumatophores are present in this zone, and oysters are absent. Grapsid crabs were present in large numbers: S. erythrodactyla in its greatest numbers on the shore; Helograpsus haswellianus was exclusively found there; P. laevis and H. leachii were present in small numbers. The ocypodid H. cordiformis was also present in minimal numbers.

The general trends in the vertical distribution on the shore of crabs at Patonga are similar to those described on other mangrove shores in places such as Java (Verwey, 1930), Brazil (Dansereau, 1947), Brisbane (Snelling, 1959), Mozambique (Macnae and Kalk, 1962), along the east coast of Australia (Macnae, 1966), Malaysia (Berry, 1963, 1972; Sasekumar, 1974), Jamaica (Warner, 1969) and Thailand (Frith et al., 1976); see pages 3-8. Species of the families Ocypodidae and Grapsidae are most numerous. Ocypodids are more abundant on the lower levels on the shore; grapsids on the higher levels. The only other family of crabs

represented on the shore at Patonga is the Xanthidae; the xanthid, P. serratifrons was found exclusively in Zone I. Xanthids have previously been found on the lower levels of mangrove shores by Dansereau, 1947, Snelling, 1959, and Warner, 1969. No species of fiddler crabs (genus Uca) were found in the mangrove swamp at Patonga. Fiddler crabs have been reported in most other mangrove swamps studied.

The only previous study specifically designed to investigate quantitatively the vertical distribution on the shore of crabs in a mangrove swamp was that of Warner (1969). The zonation found in the present study is very similar to the pattern of three zones on a shore described by Warner (see page 6). The presence of some species in greatest numbers on lower levels on the shore and in decreasing numbers towards the higher levels, and the presence of other species in greatest numbers on higher levels on the shore and in decreasing numbers towards lower levels on the shore, is common to both studies. Warner (1969) considered that such a pattern of distribution arose because of the rather more rapid changes in the environment at high tide and low tide levels than in between. Similar patterns of distribution have been found on other types of shore (Stephenson and Stephenson, 1949).

Many of the species of crabs in the mangrove swamp at Patonga occupy specific microhabitats within the zone or zones where they are present. All the different places on the floor of the swamp which are suitable habitats for crabs are occupied. The oysters in Zone I provide shelter for P. serratifrons and P. laevis (particularly gravid females during the breeding season,

see page 68). Fallen timber and other debris, and the roots at the base of mangrove trees provide refuge for large numbers of S. erythrodactyla. Depressions in the soil (often beneath fallen timber) in which the soil is of very high moisture content or which retain puddles of water at low tide, provide places for the entrances to burrows of S. erythrodactyla and probably P. laevis. Open spaces on the swamp floor, particularly in the lower zones, are covered with entrances to the vertical burrows of the ocypodids, H. cordiformis and A. tridentata. Much of the space beneath the swamp floor is taken up by the extensive systems of burrows occupied by the grapsids. The presence of suitable microhabitats in the mangroves at Patonga appears to be as important to the distribution of crabs as has been described in other places (Snelling, 1959; Warner, 1969; Frith et al., 1976).

The vertical positions on the shore occupied by the species of crabs at Patonga are similar to the positions occupied by the same species on other shores (see pages 4-8). S. erythrodactyla and H. haswellianus have both been found to occupy positions high on the shore, where they live beneath debris or else dig burrows (Snelling, 1959; Ono, 1959; Griffin, 1971). P. laevis was found lower on the shore by both Snelling (1959) and Griffin (1971). I. paludicola and P. serratfrons were found living under debris at low tide level and A. tridentata was also found at lower levels on the shore living under stones, if they were present, but otherwise digging burrows (Snelling, 1959). The positions on the shore in which H. cordiformis build their vertical burrows have been noted by Snelling (1959), Macnae (1966) and Griffin (1968, 1971).

The changes in the relative abundance of the species of crabs at Patonga have already been discussed with respect to the data obtained from the sampling programme (Section 3.34, page 70). In most cases the period of greatest relative abundance of crabs was in the warmer months of the year and this corresponded to the time when gravid females were present. Comparison with the data from Section 4 confirmed that this was so for S. erythrodactyla (page 112). P. laevis was found in greatest numbers during winter, when they breed. Again the data in Section 4 (page 113) confirmed this. Greatest numbers of H. cordiformis were found during the summer months. This, however, contrasts with the data on breeding seasons for this species as described in Section 4 (page 112). H. cordiformis breeds throughout the year, but the lowest numbers of gravid females and the lowest percentages of mature oocytes in the ovaries were present in summer, when relative abundance of crabs was greatest. It appears that for all species except P. laevis and H. cordiformis increasing activity is related to increases in air temperature and the onset of the breeding season. For P. laevis, however, the timing of the breeding season may dictate when activity is greatest. For H. cordiformis, the breeding season and the period of greatest activity are apparently unrelated.

At the southern limit of the distribution of H. cordiformis, in Tasmania, the timing of the breeding season and period of greatest activity of this species were related. H. cordiformis were most active during the summer months; activity during winter was at a very low level (Griffin, 1968). In Tasmania, H. cordiformis only breeds in summer (Griffin, 1971). The colder tem-

peratures encountered in winter in Tasmania probably restrict the breeding of H. cordiformis to summer. The period of greatest activity and breeding season of another ocypodid in Tasmania, Hemiplax latifrons, also coincided in this way. Both reached a peak in the warmer months of the year (Griffin 1968, 1971). A number of other studies of the breeding seasons of crabs have been made (these are discussed on page 122) but they do not relate breeding seasons to the general level of activity of the populations of crabs. Any differences between the times of greatest activity during the year and the peaks in the breeding cycles cannot, thus, be determined.

Changes in the vertical distributions of crabs on the shore have been observed. The possible migrations of gravid P. laevis and S. erythrodactyla females to lower levels on the shore to spawn have been postulated (pages 67, 68). These would be similar to the breeding migrations observed by Warner (1967), in Jamaica, and Ono (1959), in Japan, in which female Aratus pisoni and Sesarma hematocheir, respectively, moved to lower levels to spawn. Gifford (1962) also described the migration of the tropical land crab Cardisoma guanhumi to the water's edge to spawn.

There appears to be little correlation between breeding seasons and vertical distribution of crabs on the shore at Patonga. Most of the species breed in summer. Of the two most abundant and largest species on the lower levels on the shore, P. laevis breeds only in winter, and H. cordiformis has a peak of breeding in winter. Any significance of this pattern is unknown. Comparison with studies of the reproductive cycles

of other species of crabs indicate that most crabs have definite breeding seasons. This has been found true for: Pachygrapsus crassipes on the west coast of North America (Hiatt, 1948); Cardisoma guanhumi in Florida (Gifford, 1962); two species of Hemigrapsus on the west coast of North America (Knudson, 1964); a number of grapsids in Jamaica (Hartnoll, 1964, 1965); Cyclograpsus granulosus and Brachynotus spinosus in Tasmania (Griffin, 1969); Carcinus maenas at Plymouth, England, (Naylor, 1962). The South African grapsid, Cyclograpsus punctatus, has been found to have two breeding periods (Broekhuysen, 1941). The only report of crabs breeding throughout the year was that of Warner (1967) in Jamaica. Aratus pisoni breeds throughout the year in phase with a lunar rhythm, so that eggs hatch at full and new moon. Warner (1967) considered that the absence of large seasonal fluctuations in temperature in Jamaica might be the reason for A. pisoni breeding throughout the year. Goodbody (1961) found this to be the case with many tropical animals.

Factors that might be important in determining the distributions of the four most abundant species of crabs in the mangrove swamp at Patonga were investigated. Salinity and the concentration of organic matter in the soil were found to be unimportant. All four species of crabs showed a strong preference to settle on soil of high rather than low moisture content. Correlation between the distributions of three of these species, H. cordiformis, A. tridentata and P. laevis, and variations in moisture content of the soil and factors influencing this (i.e. depth to the water table and period of exposure to air), indicated that moisture content of the soil

is an important determinant of the distribution of these three species.

A. tridentata are small crabs which feed on the surface at low tide and were less able to resist desiccation than the other species. They were most abundant in zones lower on the shore (Fig. 3-15). Snelling (1959) also concluded that the moisture content of the soil was important in determining the distribution of A. tridentata.

The numbers of H. cordiformis were also greatest lower on the shore and decreased in zones higher on the shore (Fig. 3-15). Moisture content of the soil appears to be more important in determining the distribution of H. cordiformis than the composition of particle sizes of the soil. H. cordiformis can probably feed equally well on soils of both compositions of particle size present in the study site at Patonga, due to the morphological adaptations of their mouthparts (see page 92). The role of the particle sizes in the soil in determining the distribution of H. cordiformis is thus less important than has been found for other ocypodids, particularly of the genus Uca (Crane, 1941, 1975; Altevogt, 1957; Teal, 1958; Miller, 1961; Ono, 1962, 1965; Cameron, 1966; Macnae, 1968; Frey et al., 1976).

The greatest numbers of P. laevis were found in Zones I and II (Fig. 3-15). These grapsids showed a preference for soil of high rather than low moisture content. The ability of P. laevis to resist desiccation is possibly less than H. cordiformis and S. erythrodactyla. The vertical distribution of P. laevis on the shore is thus probably determined to a large extent by the moisture content of the soil. The penetration of

zones higher on the shore by small numbers of P. laevis may be possible due to nocturnal behaviour, occupation of the networks of large tunnels beneath the floor of the swamp and adaptations to breathing in air (see page 93). Reproductive condition may also be important in determining the vertical distribution of female P. laevis. It has been postulated that some movements to zones lower on the shore of females of this species occur during the breeding season (see page 67).

The important factors influencing the distribution of S. erythrodactyla on the shore at Patonga are less clear than for the other three species. S. erythrodactyla showed a preference for soil of high moisture content. This species was more abundant in those zones higher on the shore where soil moisture content was lower (Fig. 3-15). S. erythrodactyla also showed a preference for soil with a lower percentage of fine particles (as is present in Zones II, III and IV). This preference, however, cannot explain why the numbers of S. erythrodactyla increase uniformly from Zone II to Zone IV. Several factors obviously aid the penetration of higher levels on the shore by S. erythrodactyla. These include adaptations to breathing air (see page 93), great tolerance to low humidities, nocturnal behaviour, occupation of networks of burrows and tunnels beneath the floor of the swamp, use of timber and other debris for cover during the day at low tide, and use of depressions containing moist soil as places in which to dig burrow entrances. In addition, the vertical distribution of S. erythrodactyla may be influenced by the reproductive condition of females. A migration of gravid S. erythrodactyla to lower levels on the shore during the breeding season has been postulated (see page 67).

Of the factors which other workers have suggested influence the vertical distribution of crabs on mangrove shores (see pages 11-13) it has been shown that salinity and the organic content of the soil are not important at Patonga. Temperature and hydrogen-ion concentrations of the water were found unimportant by Sasekumar (1974) and Frith *et al*. (1976). These were also considered to be unimportant at Patonga because of the great daily fluctuations in these variables. They were not examined in this study. Temperature variations would be fairly uniform over the swamp as it is all in the shade of the mangrove trees. Particle-size of the soil is also probably unimportant, as has been discussed. The moisture content of the soil appears to be important in the distribution of three species of crabs. This was also considered important by Snelling (1959) and Sasekumar (1974). Factors such as length of period of exposure to air and depth to the water table are possibly important in influencing the distribution of these same three species at Patonga, only because of their influence on the moisture content of the soil and their influence on the desiccation that crabs might experience. The presence of suitable microhabitats in which crabs can live is probably also important in influencing the distribution of crabs, particularly grapsids.

Clearly, more work is needed to establish the roles of other factors in determining the vertical distribution of crabs at Patonga, especially *S. erythrodactyla*. It is apparent that the distribution of different species of crabs may be influenced by different factors. It is also possible that the

distribution of a species in a particular place may be influenced by factors which differ from those that limit its distribution in another place. Predation, both by herons and by crabs, was occasionally observed during the study, but was considered unimportant. S. erythrodactyla and P. laevis were seen to prey upon H. cordiformis and S. erythrodactyla. The remains of small P. laevis were found within the stomachs of larger numbers of the same species. Interspecific competition for food and space could be important. This was suggested as having some influence on the distribution of H. cordiformis (page 93). Ono (1962) also considered that interspecific competition was important in determining the distribution of ocypodids. The density of crabs at Patonga is great and the activity of all species, with the exception of P. laevis, is greatest at the same time of the year. Interspecific competition may therefore be important in determining the distribution of crabs between zones, or, at least, within zones. In addition, length of period of exposure to air may have some influence on the distribution of S. erythrodactyla. (see page 92). It may influence the suitability of the soil as a place in which S. erythrodactyla can dig burrows or be important in determining the time available for crabs of this species to look for food. Ono (1959, 1962) suggested that length of period of exposure to air determined the vertical distributions of grapsids and ocypodids as a whole, although it did not determine the distribution of individual species of ocypodids.

Thus, while the mangrove study site at Patonga differs in many fundamental ways from more complex mangrove swamps

closer to the Tropics, it shows several major similarities of distribution of its crab fauna. A more complete understanding of the ecology of the crabs at Patonga might be gained by further studies including:

(i) more quantitative sampling, possibly using a greater number of traps in each zone, and, perhaps, the development of a mark-recapture programme to investigate more fully the breeding migrations suggested in this study;

(ii) the experimental investigation of those factors, such as predation and interspecific competition, which might have some effect on the distribution of crabs.

Finally, it is suggested that the sampling techniques developed in this study might be used with success in sampling crabs on more complex mangrove shores.

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