4. THE ZONATION OF ROCKY LITTORAL AREAS AROUND LITTLE CAYMAN

G.W. Potts

Abstract

The distribution of the rocky littoral fauna at sites representing different degrees of exposure were examined around Little Cayman. It was found that the molluscan species composition, species morphology and vertical distribution was affected by the exposure of a particular site.

Introduction

During July and August 1975 the Royal Society and Cayman Island Government supported an expedition to Little Cayman where aspects of the ecology of the island were studied. The Cayman Islands (between 19°15'N and 19°45'N latitude and 79°44' and 81°27'W longitude) are composed of three limestone islands which are formed by the projecting peaks of a range of submarine mountains that form the Cayman Ridge to the north west of Jamaica. According to Matley (1926) the central part of each island is comprised of an old "Bluff Limestone" while the periphery is made up of a mixture of coral sand, marl, and elevated limestone reef which has been weathered to form what is called the "Ironshore formation" (Doran 1954, Idyll, 1966). The limestone shore is extensively eroded by the action of rain, the sea, and also the grazing action of some littoral molluscs and the abrasive action of the shells or spines of some species of mollusc and echinoderm, as described by Ginsburg (1953) for the Florida Keys region. It was this rock that was examined in the present work on littoral zonation. The Cayman Islands are particularly interesting because they form a discrete island unit lying in deep water midway between Jamaica, Cuba and the northern coast of South America and yet there have been few studies specifically relating to the littoral region to these islands. Abbott (1958) provides the most important contribution to the marine molluscs of Grand Cayman and includes brief ecological notes in conjunction with a reasonably comprehensive species list. The zonation of littoral species on Little Cayman has not been studied before although it is to be

Atoll Research Bulletin No. 241: 23-42, 1980.

expected that in general terms it would be similar to that described for Grand Cayman (Abbott 1958) and for other areas of the Caribbean (Stephenson and Stephenson (1950, 1952), Coomans (1958), Voss and Voss (1955), Bakus (1968), Bakus (1975), and others). Nonetheless the survey did produce new records from a hitherto unstudied island with data on the influence of exposure on littoral rock faunas.

Methods

A number of areas were selected around Little Cayman to demonstrate the zonation of littoral animals (Figure 11). Each area was examined for species composition, distribution and abundance and then the profiles were drawn of the shore from the low water notch to above the strand line which occurred approximately one metre above the level of high water. Special attention was paid to the distribution of species in relation to their vertical zonation at sites on the leeward and windward shores. The influence of exposure and wave action were studied by selecting suitable boulders and assessing the distribution of molluscs on the seaward and landward faces of these rocks. Unfortunately time did not permit taking physical measurements of exposure which is here based upon the interpretation of such features as coral type, presence and extent of a storm beach, reef development, nature of particulate substrates as well as meteorological data.

No published tidal data was found for Little Cayman, however it is unlikely that it will differ significantly from the Admiralty Tide Table predictions for George Town, Grand Cayman (fig. 12) and this has been used as the basis for assessing the tidal levels.

Fig. 12 gives the fluctuations in tidal height throughout the period of the expedition together with the hour by hour changes in tidal height on a spring tide and on a neap tide. In areas with such a small tidal amplitude it is probable that local coastal morphology and meteorological conditions are more important in influencing the zonation of the fauna and flora than the tidal range (Gosline, 1965). The sites selected for examination represent a range of exposures from the extreme shelter of Owen Island within South Hole Sound to the exposed Bluff at East End, and several sites representing the intermediate exposure types. The sites examined were; in order from sheltered to more exposed sites; Owen Island within South Hole Sound, Jackson's Bay Rocks, Preston Bay, Rubble ridge that encloses South Hole Sound, West End Point rocks and the Bluff at East End.

While several groups of marine biota were represented in the littoral of Little Cayman the present survey deals in the main with the mollusca and decapod crustacea. Where possible provisional field identifications were made and samples taken for checking upon return. The following authorities have been consulted when identifying specific groups; molluscs, Warmke and Abbott (1961) Morris (1973); Neritidae, Russell (1941); the *Littorina ziczac* "complex", Borkowski and Borkowski (1969); hermit crabs, Provenzano (1959); stomatopods, Manning (1968); marine algae, Chapman (1963); and marine angiosperms, den Hartog (1970). The terminology used to describe the shore zones follows

Stephenson and Stephenson (1950).

Results

The results of the field surveys are outlined below, first describing the different survey sites, a comparative note on the size distribution of intertidal mollusca in relation to exposure. Finally the work is discussed in relation to other surveys from this region.

Preston Bay

Preston Bay (Plate 22) is on the South West side of Little Cayman and consists of a sand and coral rubble beach with occasional outcrops of eroded limestone. Beyond this littoral zone is the sublittoral upper reef terrace which varies between 200 and 400 m wide and which terminates on the seaward side with a coral buttress zone which itself is followed by a lower reef terrace. In addition to the limestone beach outcrop a small concrete jetty was examined.

Fig. 3 shows the profile of a representative rock outcrop from this region and also indicates the distribution pattern of the most important species. Above the beach rock is the supralittoral fringe comprising coral sand and coarse coral rubble. This mobile substrate was devoid of macrofaunal elements except in some areas of sand in which the burrowing crab, *Ocypode* sp. (probably *O. quadrata* (Fabricius)) was to be found. The only mollusc that occurred in this region was *Tectarius muricatus* on wood on the strand line and occasionally on coastal shrubs, such as *Suriana maritima* (L.), *Borrichia arborescens* (L.) DC. and others.

The rocks of the upper midlittoral zone contain species that depend upon periods of submergence for their survival. The most active is the crab, *Grapsus grapsus* (L.) which was common wherever rocks extend into this region. One specimen of *Goniopsis cruentata* (Latreille) was also found although it is more frequently associated with estuarine muds (Chace and Hobbs, 1969). The littoral gastropods *Echininus nodulosus, Nodilittorina tuberculata* (Plate 24) are tolerant of the more exposed conditions found on the dry surfaces of upward facing rocks, while *Littorina ziczac* and *L. lineata* are usually found in crevices, coming out and moving over the rock surfaces when the rocks are wet or at high tide. Where *L. ziczac* is found it may occur in large numbers and estimates of 1700 per square m were made where the substrate type and crevices provide suitable habitats. It was not possible to distinguish between *L. ziczac, L. lineolata* and *L. lineata* in the field so for these and subsequent population estimates they have been grouped together (see Borkowski and Borkowski 1969). Although samples from the different areas indicated which species were present. *E. nodulosus* was not as numerous and reached a maximum density of approximately 500 per square m. Both *L. ziczac* and *E. nodulosus* had patchy distributions and over most of the area their densities were much lower than those mentioned above. *Nodilittorina tuberculata* like *E. nodulosus* was distributed over the upper faces of the rocks and occupied much the same tidal level. It was interesting to note that despite the similarity in habitat between these species, it was unusual to find these species together on the rock (see Abbott 1954 and comments on the distribution of these species).

The lower midlittoral zone is occuped in the main by nerites (Plate 26), but also contains faunistic elements of the upper midlittoral zone on rocks that drain and dry quickly, and infralittoral fringe species less tolerant of exposure to air. At Preston Bay *Nerita versicolor* occurred in the upper midlittoral zone and extended down to nearly low water mark. This species had the widest range of any of the littoral gastropods and was dominant in the upper levels of the lower midlittoral zone. The mid-tide level rock pools were occupied in the main by *Nerita tessellata* which over small areas was found in densities of over 200 per square m. On this particular beach *N. peroronta* was infrequent and a few only were found at about mid-tide level in rock pools or at the edges of them together with *Littorina meleagris*.

On the lower part of the midlittoral zone in both pools and on the open rocks was the chiton, *Acanthopleura granulata* which with *N. tesselata* were the dominant species at low water. The infralittoral fringe contained a wave cut notch that was subjected to strong wave action and which showed an increased species diversity. Here the first macroscopic algae were found and the intrusion of some members of the immediate sublittoral benthic communities. On the low water notch *Cittarium pica* and *Purpura patula* were found, the former reaching densities in excess of 40 per square m; but the convoluted nature of the shore made it impossible to do more than estimate at the population density. *P. patula* was less common. On the larger specimens of *C. pica* specimens of the limpet *Acmaea leucopleura* were frequently to be found at the edge of the body whirl adjacent to the columella. None of these sucker limpets were found on *C. pica* that was less than 4 cm in shell length although some were found free on the nearby rocks of the low water ridge. In the low level rock pools and along the infralittoral fringe specimens of *Echinometra lucunter* (L.) and less commonly *Diadema antillarum* (Philippi) were found, while in the sublittoral region *Echinometra* reached densities of approximately 50 per square m in the numerous crevices and fissures of the sublittoral rock.

A single specimen of each of *Tegula fasciata* and *Clathrodillia melanesiana* were found in the lower midlittoral zone. Beneath large stones in the lower midlittoral zone and in the infralittoral fringe the Tree oyster, *Isognomon radiatus* was not uncommon. Small specimens of the brittle star, *Ophiocoma echinata* (Lam.) were sometimes found beneath stones in littoral pools while larger specimens were found beneath stones over the upper reef terrace together with *O. pumila* (Lam.).

The rock pools and the immediate sublittoral rock contained most commonly the algae *Acetabularia crenulata* Lamx., *Padina sanctae-crucis* Børg. and an unidentified species of *Dictyota* sp., together with patches of *Turbinaria turbinata* Bart. which was also frequently washed ashore in wave swept areas.

The infralittoral fringe shows the beginning of the fauna of the upper reef terrace with corals tolerant of turbid conditions, *Siderastraea siderea* (Ellis & Sol.), *Millepora complanata* L. and others. Where the substrate is finely particulate the eel grass *Thalassia testudinum* König may come close to low water mark densely covering the area. *Syringodium filiformis* Kütz. was also found associated with *T. testudinum* in inshore areas.

Preston Bay Jetty

Within Preston Bay was a small concrete jetty 18 m long and 1.60 m wide. The alignment was approximately North South and its slope was 20 cm over its length ending 20 cm above LWMST at the southern end. The prevailing wind was from the South East and the water movement on the reef flat was from East to West so that the east side of the jetty was subjected to greater turbulence than the west side.

The distribution of gastropods reflected the difference in the exposure on the two sides of the jetty and clearly demonstrated that wave action and water movement will have a greater effect on the distribution of littoral species than the tidal amplitude. Fig. 14 indicates how the distribution varied along the jetty and from the exposed East side to the sheltered West side. This distribution is particularly striking as the jetty presented a relatively uniform substrate type without the numerous crevices of the surrounding rocks.

The species recorded from the jetty included *L. ziczac, N. versicolor, N. peloronta, N. tesselata, A. granulata, C. pica* (Plate 30) and *P. patula*. These gastropods were mainly living on the vertical walls of the jetty at each side. At high tide or when wave action was sufficient to cause the top of the jetty to be awash, the gastropods would move about over the horizontal surface. The crab, *Callinectes* sp. was seen below the tide level on the sides of the jetty while *Grapsus grapsus* was found in the upper midlittoral region.

West End Rocks

West End Point (Plate 23) consisted of a rock plateau below a sandy beach. The rock was several hundred metres in extent and contained several large rock pools which were examined. A profile of the rock is given in fig. 15 together with the distribution of the most common littoral species. To the South and East of the area a steeply sloping shingle and coral rubble beach exists and which joins a series of longitudinal limestone outcrops which slope to the seawards and which project from the shallow sublittoral of the upper reef terrace to a height approximately equal to HTL. These ledges join the rubble beach and extend Eastwards to join Preston Bay and the Preston Bay Inshore formations described above. To the North of West End Point rocks the particulate beach continued to join up with the extensive limestone shore at Salt Rocks.

At Preston Bay the beach is protected from the full wave energy by the buttress zone of the upper fore-reef terrace. At West End Point there is no such protective barrier and the waves break directly on the rocks below the Tower light house. It is this wave action that replenishes rock pools in the midlittoral zone with seawater more frequently than would be expected by tidal movement alone.

The supralittoral fringe contained a strandline of wood debris with few marine species, and only *Tectarius muricatus* was found in abundance, although even this species was absent in areas of sand and where the drift wood rested on sand. The sand itself was highly mobile and yet contained a small population of *Ocypode* sp. The sand movement had scoured the upper midlittoral rock outcrops which were devoid of life, but below its influence *Tectarius muricatus* was found on the open rock and in dense numbers on the seawater tolerant *Sesuvium portulacastrum* L. (Plate 25). The littoral zone contained *Nodilittorina tuberculata* and *Echininus nodulosus* which were found on the exposed rock faces and in moist crevices together with *Littorina ziczac* and *L. lineata*.

The lower midlittoral species were more numerous than at Preston Bay and several species were abundant that were hardly represented at this former site. Once more the nerites, *N. peloronta, N. versicolor* and *N. tessellata* were common (Plate 26) and in particular *N.tessellata* which favours the rock pool habitat. In addition to these, the zebra nerite (*Puperita pupa*) and *Littorina mespillum* were found in large numbers in rock-pools (see Plates 34 and 35).

The lower midlittoral zone was more dissected than at Preston Bay Rocks and contained a greater density of molluscs. *N. tessellata* extends down to the low water notch where *C. pica, A. granulata* become the dominant mollusca. In the low water pools occasional *Echinometra lucunter* and *Diadema antillarum* were found. The low water concentrations of *Echinometra* increased in the sublittoral and reached densities equivalent to the sublittoral region of Preston Bay (50/sq m). Owing to the turbulent conditions on West End Point it was not possible to examine the immediate sublittoral from the seaward, but inspection at extreme low water showed that the algae were similar to those at Preston Bay with *Acetabularia crenata, Padina sanctae-crucis, Dictyota* sp., and *Turbinaria turbinata* were common, growing sparsely in the low level rock pools.

In this region the extent of the distribution of molluscs is affected by the increased exposure of this site. The greater wave action not only increases the height to which certain midlittoral species will extend, but also has a profound influence upon the pool faunas. The mollusca *Planaxis nucleus, P. plineatus, Litiopa melanostoma* and *Tegula excavata* were only found at this site at low tide level.

The hermit crab *Clibanarius tricolor* (Gibbes) was common and often very abundant in mid-tide level pools in the shells of *Echininus nodulosus, Nodilittorina tuberculata, Littorina ziczac* and *Cerithium variabile*.

Bloody Bay and Jackson's Point

In this region the upper shore consists of a poorly developed storm beach or coral boulders and rubble which rises to a height of 2 m above mid-tide level. Below this is a sand or sand and rubble beach that extends into the littoral region and in some areas onto the upper fore-reef terrace of the sublittoral region (Fig. 16). Occasional outcrops of rock provide the solid substrate essential for the development of a littoral zonation and two of these were examined.

The coastal fringe consisted mainly of sea grape (*Coccoloba uvifera* (L.) L.) except where an area had been cleared to provide the basis for a coconut plantation. In some suitable areas *Scaevola plumieri* (L.) Vahl, *Suriana maritima* and *Sesuvium portulacastrum* L. extended down to high water mark and on these *Tectarius muricatus* were found in some members. This high level gastropod was also found up to 2 m above MTL upon the driftwood of the supralittoral fringe. The first truly littoral molluscs, *E. nodulosus, L. tuberculata, L. ziczac* and *L. lineata* were only present in small numbers on the rocks, but did occur on the tops of large boulders in the littoral region where they would be subjected to the periodic splash from waves. The lower midlittoral is more extensive than at West End Point or Preston Bay and *Nerita versicolor* and *Acanthopleura granulata* (Plate 33) were particularly abundant both reaching densities in excess of 40-50 per sq m. *N. tessellata* and *N. peloronta* were present in the permanent pools of the lower midlittoral zone and *Cittarium pica* was found along the infralittoral fringe under and among the stones and ledges of this zone. Jackson's Point was not subjected to heavy wave action despite the absence of rubble ridge. Fig. 16 shows a section of the shore at Jackson's Point and the distribution of the most common species.

At Jackson's Point the distribution of gastropods around a large boulder was examined to see if the aspect and orientation had an effect upon their distribution. Fig. 17 shows a profile of this boulder and the distribution of some species that were on it. It is seen that the upper midlittoral species *E. nodulosus* and *L. ziczac* are unaffected in their tidal level regardless of the aspect of the boulder. However, the zonation of the lower midlittoral species *A. granulata* and *C. pica* indicates a higher tidal distribution on the seaward side where they would be subjected to greater wave splash. By contrast the nerites occurred on the sheltered landward side of the rock with *N. tessallata* slightly higher than *N. versicolor* and *N. peloronta*. The infralittoral fringe contained the alga *Valonia* sp. and in rock crevices *Echinometra lucunter* was common around the boulder.

The Bluff — East End

The East End of Little Cayman (Plate 29) consists of the Bluff Limestone, a weathered and dissected rock outcrop in the littoral region and with a storm beach of coral rubble behind the ironshore. The site is very exposed to south east winds.

A diagram of the distribution of the common species is given in Fig. 18. While the densities of mollusca are very variable some maximum figures were recorded at different levels on the shore. In the supralittoral fringe on drift wood *Tectarius muricatus* was very common (Plate 32) raching densities of between 144 and 152 per square m while on the rocks of the upper midlittoral zone densities of between 32 and 56 per square m were typical. *Nodilittorina tuberculata* reached densities of 60 per square m and in rock pools *L. mespillum* occurred at over 168 per square m. Nerites were present in the littoral zone, but in smaller concentrations than the more sheltered shores in the south and west of the Island. They tended to concentrate at the margins of rock pools of the midlittoral zone. *N. versicolor* was the most common and *N. tessellata* occupying the same region was less abundant. *N. peloronta* was more widely distributed although at lower densities. The other species commonly associated with rock pools was the small littorinid, *Littorina mespillum* which was usually evenly distributed over the pool. *Acanthopleura granulata* and *C. pica* were common at low water level occurring in densities of 24 and 36 per square m respectively while *Purpura patula* was only found at low water and on the low water notch at densities between 2 and 10 per square m.

With the increase in wave action at the east end of Little Cayman several species were present that were not recorded from more sheltered sites. The most abundant in the lower midlittoral region was the mussel *Brachidontes exustus* that was common in crevices of this region. Others recorded were *Isognomon alatus, Coralliophylla abbreviata* and an unidentified species of vermetid.

Rubble Ridge

On the south side of Little Cayman running almost the whole length of the island the fringing reef is separated from the seaward terraces by a ridge of coral rock and rubble (Plate 29). This ridge does not seem to be comparable to the algal ridges of Indo Pacific atolls, and comprises of boulders ranging from a few cms up to about a metre in diameter. The ridge was breached in several places forming channels from the sea into the shallow lagoon, South Hole Sound. Waves splashed over the ridge in many places and at high tide almost the entire zone was covered in sea water and subjected to considerable wave action. Small patches of the black and red mangrove grew on the inside edge of the rubble ridge. The molluscan zonation on the ridge was similar to the ironshore outcrops described above except that there was no equivalent to the supralittoral zone. The zonation was only found on the seaward side of the ridge and not on the lagoonal side where apparently the lack of water movement and the consequent silting prevented the development of a rocky shore molluscan fauna.

The lagoonal beach of the rubble ridge consisted of sand or fine mud generally with *Thalassia testudinum* growing in dense patches immediately below low water. This was replaced by silted coral rubble upon which a yellow algae film covered large areas and in which mangroves had begun to grow. The central part of the ridge contained the largest boulders and it was this region that contained the upper midlittoral fauna with *Tectarius muricatus* and in crevices *Littorina ziczac* and *L. lineata*. At the same level, but in more shaded situations, *Echininus nodulosus* and *N. tuberculata* were found, while under stones and in the moist areas between the boulders *Nerita tessellata* and *N. versicolor* were common together with grapsid and porcellanid crabs. On the outer rubble beach on the seaward side of the ridge, nerites were still common but with the increase in water movement *Cittarium pica* and *Acanthopleura granulata* became more abundant until at low water mark and in low areas of the ridge where water streamed from the seaward side of the ridge to the lagoon these two species became the dominant molluscs. *Cittarium pica* on the rubble ridge was covered in calcareous algae while those associated with the Preston Bay jetty were relatively clean (Plates 30 & 31). It is interesting to note that despite extensive searches neither *Nerita peloronta* nor *Purpura patula* were found. Beneath stones at the lowest levels *Echinometra lucunter* and *Isognomon radiatus,* were found, the echinoid extending in greater densities into the sublittoral.

Owen Island

Owen Island lies within South Hole Sound and is sheltered from the open sea by the rubble ridge (see above). The Island was not extensively studied, but samples of the common mollusca were collected. The typical rocky shore mollusca were present, but representatives of the low water species, *Cittarium pica* and *Purpura patula* were absent as were the littoral pool species. In the black mangrove areas to the north of Owen Island *Littorina angulifera* was common and among the roots the crab *Callinectes marginatus* was frequently seen.

The remaining molusc *Cerithium literatum* recorded from Owen Island is one that is characteristic of the *Thalassia* beds that are plentiful around this Island.

Size distribution of littoral mollusca in relation to exposure

In Table 3 the mean sizes of the common littoral mollusca are given against the sites from which they were collected. The sites are arranged from the most sheltered at Owne Island to the most exposed on the Bluff end of the island at East End. While some of the sample sizes are inadequate to draw clear conclusions from, some general trends are present which indicate the relationship between exposure and molluscan distribution and morphology. In the first place the high level *Tectarius muricatus* does not have any significant size differences between the sheltered and exposed sites. Only on the Rubble Ridge of the South Hole Sand was a small record found from a single specimen. The site is generally too low for this species, never extending as high as the supralittoral fringe and the specimen found cannot be considered representative. *Littorina mespillum* was found at too few sites to give any indication of the effect of exposure on body size, but it would be expected to be slight in view of the fact the species is mostly restricted to pools. The same can be said of *Puperita pupa* which is also confined to rock pools and was only found at the rocks at West End.

Table 3. Size distribution of the Common littoral Mollusca around Little Cayman

	Tectarius muricatus	*Nodilittorina tuberculata*	*Echininus nodulosa*	*Littorina ziczac*	*L. lineata*	*L. lineolata*	*L. mespillum*	*Nerita versicolor*	*N. tessellata*	*N. peloronta*	*Puperita pupa*	*Cittarium pica*	*Purpura patula*	*Acanthopleura granulata*
Owen Island	16.8 (32)	11.4 (17)	11.1 (58)	16.1 (4)	7.8 (3)	10.2 (2)	-	21.8 (20	23.0 (1)	23.7 (10)	-	-	-	-
Jackson Bay	16.3 (8)	7.4 (5)	-	11.1 (2)	7.6 (3)	-	-	10.7 (6)	10.0 (2)	13.5 (2)	-	21.0 (5)	-	93.5 (8)
Preston Bay	-	-	10.7 (6)	11.2 (13)	6.7 (20)	-	-	14.4 (14)	10.6 (13)	22.3 (12)	-	14.8 (135)	42.5 (4)	69.8 (4)
Rubble Ridge	8.0 (1)	6.6 (12)	10.1 (9)	11.8 (1)	6.7 (5)	-	-	16.0 (10)	13.8 (21)	12.0 (2)	-	13.8 (24)	-	-
West End	-	6.6 (57)	11.4 (20)	-	3.9 (5)	-	2.5 (29)	-	-	17.0 (3)	6.1 (65)	-	-	-
East End	17.2 (21)	5.6 (45)	-	7.7 (15)	4.6 (7)	5.3 (2)	2.4 (5)	10.6 (9)	7.2 (38)	13.7 (14)	-	20.8 (104)	29.0 (9)	59.7 (7)

The figures in the body of the table represent the mean size in (mm) of named molluscs. The sample size is given in brackets beneath each size. The absence of figures does not mean that a species did not occur at a site but that a sample was not collected and measured.

With the exception of *Echininus nodulosa* the littorinids showed a gradation in size with increasing exposure. Thus *Nodilittorina tuberculata, Littorina ziczac, L. lineata* and *L. lineolata* all showed a decrease in size on more exposed sites. The same general trend was shown with *Purpura patula* and *Acanthopleura granulata*. The nerites, *Nerita versicolor, N. tessellata* and *N. peloronta* did not show a clear relationship with the exposure of a site, but each of these species was very large at Owen Island, the most sheltered site. It can only be assumed that perhaps the sheltered nature of this site or some other factor than the direct influence of exposure was responsible for the large Owen Island specimens. *Cittarium pica* is most frequently found at the infralittoral notch and in two fairly extensive searches and collections at Preston Bay and East End showed that specimens were larger at the more exposed East End. *Cittarium* apparently favours turbulent conditions and constant water movement as is shown by its habitat preference and size distribution. What is surprising is the large mean size of those individuals on the Rubble Ridge of South Hole Sound which appears to result from the absence of very small individuals found at the other sites.

It is interesting to note that with the absence of brackish areas around the coast, the nerite *Nerita fulgurans* was absent. This was predicted by Russell (1941) who pointed out that with its preference for brackish estuarine and habour conditions it was unlikely to be found on the smaller islands of the Caribbean.

Rock Pool Faunas

Despite a small tidal range there were several areas where permanent littoral rock pools existed and which had an interesting and varied fauna and flora. The environment that these pools offered must have been subjected to a wide range of temperatures and salinity and these factors are likely to be important in influencing the species found in these pools. Two areas containing rock pools were examined, one at West End rocks (Plate 23) and the other in Jackson's Bay and from both areas specimens of the gastropods were collected and their zonation noted.

The littoral rock pools fall into three main types; the high level, mid tide and low level pools, and each is characterised by the type of fauna and flora present. It is not possible to give precise limits upon the height above chart datum that each category may occur in, as this varies with the degree of exposure to which the shore is subjected, but in general the greater the exposure and wave action the higher will each pool type occur. High level pools were found in the supralittoral fringe and are filled only by spray from wave action or by rain, and are characterised by green and brown algal slimes and by the lack of an obvious macrofauna. These pools occur at the level of *Tectarius muricatus* which may be found on adjacent rocks, stranded wood and shrubs of the supralittoral fringe, but never in the pools. Occasionally the crab *Grapsus grapsus* retreated into the high level pools when disturbed, but mostly they remained without a macrofauna.

The pools of the midlittoral zone were subjected to changes of water with each tide and on the exposed western end rocks to occasional replenishment from wave action. These pools were characterised by a varied gastropod fauna and occasionally some contained very large numbers of the hermit crab *Clibanarius tricolor*. Young fish were common and the litoral goby *Bathygobius soporator* was present in all permanent rock pools. The pools in the lower midlittoral zone were subjected to constant wave action and the faunal elements may contain an occasional representative washed in during rough conditions from the infralittoral fringe and the sublittoral region. Occasional algae were found including *Acetabularia crenulata* which was noticeably more common in the low level pools which with *Dictyota* sp., *Turbinaria turbinata, Padina sanctae-crucis* and others were typical of the infralittoral fringe and upper reef terrace. Stomatopods of the genera *Gonadactylus* and *Pseudosquilla* were also frequently found in the crevices within the pools.

Discussion

The water eroded limestone of the littoral region provides an interesting and diverse habitat for marine molluscs around many tropical atolls and islands. Despite the often limited tidal range a distinct zonation is found from high to low water mark, and has been the subject of reviews by Stephenson and Stephenson (1950, 1952), Southward (1958) and Lewis (1960). These works together with more detailed surveys such as those by Voss and Voss (1955, 1960), Arnow, St Clair and Arnow (1963), Houbrick (1968) and others have described the distribution and vertical zonation of littoral animals in the Caribbean. Vermeij (1973) also considers the distribution of littoral molluscs in his attempt to relate their morphological differences with habitat preferences. However, as yet, little work has been done on the Cayman Islands littoral region apart from a small and non-representative collection of molluscs made during the Oxford Universities Expedition to the Cayman Islands in 1938 (Salisbury, 1953) and the important work of Abbott (1958) who described the marine molluscan fauna of Grand Cayman. No specific records exist for Little Cayman.

While the present work does not represent a comprehensive species list of the kind offered by Abbott (1958), it does indicate the distribution and zonation of the common littoral species on the beach rock around Little Cayman in relation to the degree of exposure.

The way in which the degree of exposure influences the vertical distribution of species depends upon a number of factors, including the behavioural homeostatic mechanisms employed by the animal as well as their physiological tolerances (Lewis 1963, Fraenkel 1968, Hardin 1968, and Borkowski 1971). These factors together with morphological adaptations (North 1954) enable species to colonise and exploit widely different areas although it should be recognised that different species will often employ different mechanisms for maintaining themselves within their optimum range. In addition to the local variations in species distribution there are also zoogeographic variations of the kind described by Vermeij (1973). The present work confirms the general similarity and local variability in species composition and zonation around Little Cayman with other areas within the Caribbean. (Stephenson and Stephenson 1950, 1952). The overall zonation includes a belt of maritime shrubs along the upper part of the shore. Where these extend down towards the supralittoral fringe *Tectarius muricatus* is found either on shrubs or wood on the strandline or on high level rocks. In this supralittoral fringe grapsid crabs may be present and on rocky substrates a range of upper midlittoral littorinids that extend to below mid tide level. In the upper midlittoral zone the first nerites are present generally near pools or moist crevices where there is little risk of desiccation. These extend to the infralittoral notch where the grazing *Acanthopleura granulata* and *Cittarium pica* become the most abundant species together with the carnivorous *Purpura patula*. In more exposed regions the lower midlittoral zone is characterised by vermitids and the mussel *Brachidontes*. The development of macroscopic marine algae is usually restricted to low level pools and it is only in the sublittoral region of the upper reef terrace that they become significant.

On Little Cayman it has been possible to show how around the shores of a single island it is possible to get a different species composition and zonation pattern that relates to the degree of exposure.

This has been recorded within the Mollusca and would probably be evident in other groups when subjected to detailed examination. Not only do different shores exhibit different species composition and zonation, but also within small areas of one shore it is possible to exhibit this effect. Thus on the seaward and shoreward side of a boulder, or the exposed or sheltered sides of a jetty, different zonation levels are exhibited. By measuring molluscs from different beaches it has also been possible to show that there is a difference of size between individuals found on shores of different exposure. In fact the individual species size ranges were often larger between different sites around the Island then Vermeij (1973) found for the same species taken from different areas of their zoogeographic range. Generally speaking there was a tendency for specimens to be smaller on more exposed shores, but this was not always clear and further work is needed to confirm this. Only with *Cittarium pica* was the reverse true.

The effect of exposure on a coastline is very variable, but with increased exposure there is generally more wave action which effectively increases the tidal range (Gosline, 1965). This enables a species limited only by the need for a brief period of submersion to increase its vertical range, provided it has the necessary adaptation to tolerate the greater effect of desiccation at higher levels. This can to some extent be achieved by reducing body size, or by adopting a semi-cryptic mode of life as seen in most high tide littorinids or by developing a close textured shell that will resist water loss as found in *Tectarius muricatus*.

Table 4. Distribution of littoral Mollusca

	SPECIES	Tidal level	Presence in rock pools	Owen Island	Jackson Bay	Preston Bay	Rubble Ridge	West End	East End
Mytilidae	*Brachidontes exustus* (L.)	LML				*		*	*
Isognomidae	*Isognomon radiatus* (Anton)	LML	*						
	Isognomon alatus (Gmelin)	LML	*						*
Acmaeidae	*Acmaea antillarum* (Sby)	LML-ILF	*		*		*	*	*
	Acmaea leucopleurae (Gmelin)	LML	*			*			*
Trochidae	*Cittarium pica* (L.)	LML-ILF	*	(*)	*	*	*	(*)	*
	Tegula excavata (Lam.)	LML	*					*	
	Tegula fasciata (Born)	LML	*			*			
Neritidae	*Nerita peloronta* (L.)	LML	*	*	*	*	*	*	*
	Nerita tessellata Gmelin	LML	*	*	*	*	*	(*)	*
	Nerita versicolor Gmelin	LML	*	*	*	(*)	*	(*)	*
	Puperita pupa (L.)	ILF	*					*	
Littorinidae	*Littorina angulifera* (Lam.)	ILF		*					
	Littorina meleagris Poties & Michard	LML	*			*		*	
	Littorina mespillum Mühl	LML	*					*	*
	Littorina ziczac (Gmelin)	UML		*	*	*	*		*
	Littorina lineata d'Orbigny	UML		*	*	*	*	*	*
	Littorina lineolata d'Orbigny	UML		*					*
	Nodilittorina tuberculata (Menke)	UML		*	*	(*)	*	*	*
	Echininus nodulosus (Pfr.)	UML		*		*	*	*	
	Tectarius muricatus (L.)	SLF		*	*	(*)		(*)	*
Rissoidae	*Zebina browniana* (Orb.)	LML	*						*S
Vermetidae									*

Planaxidae	*Planaxus lineatus* (da Costa)	LML						*	
	Planaxus nucleus (Brug.)	LML						*	
Cerithiidae	*Cerithium literatum* Born	ILF	*	*					
	Cerithium variabile C.B. Adams	LML	*					*	
	Litiopa melanostoma Rang	LML	*					*	
Magilidae	*Coralliophila abbreviata* (Lam.)	LML	*						*
Thaididae	*Purpura patula* (L.)	ILF	*		*	*		(*)	*
Colombellidae	*Psarostola minor* C.B. Adams	LML	*				*		
Turridae	*Clathrodrilla melanesiana* Dall & Simpson	LML	*			*			
Cryptoplacidae	*Acanthopleura granulata* Gmelin	LML	*	(*)	*	*	(*)	(*)	*

* - specimen collected
(*) - species noted but not collected
S - shell only
UML - upper midlittoral
ILF - infralittoral fringe
SLF - supralittoral fringe
LML - lower midlittoral

Tectarius muricatus occupies the highest position of the truly marine gastropods along the strandline and it is interesting to note that the mean size did not vary significantly at different sites around the island regardless of the degree of exposure. However what did change was the height above sea level which was highest on the eastern most exposed end of Little Cayman. Along this storm beach is an extensive strand line of washed up timber and it is on this timber that the densest numbers of *T. muricatus* were found at a height that could only have been wetted by the occasional spray from rough seas during storms. In this position not only must *T. muricatus* be tolerant to the desiccating effect of the sun and wind as has been shown by Rosewater (1963), but it must also be able to tolerate the osmotic stress when wetted during rain.

The difference in species composition at any one site can be explained in terms of physiological tolerance, but it is probable that other factors are involved. Paine (1966) discusses the possible influence of predatory species and how in an area where space is at a premium, such as the littoral zone, then a reduction of predators may also create a less diverse system. The situation cannot be easily summarised in a dynamic environment like the littoral region where at high water, benthic species may be subject to predation by a range of sublittoral species, such as fish, and at low water avian or mammalian predators may become significant.

In the present work the presence of carnivorous gastropods does not appear to have any obvious effect on the molluscan diversity, but it is possible a more extensive survey would be necessary to be certain.

While there is a useful literature on the littoral faunas of the Caribbean rather few actually mention the significance of rock pools in this region. North (1954) comments on the erosion of pools as a result of wave action, but adds little to the understanding of these important littoral habitats. Houbrick (1968) recognises their importance in the coastal zone of Costa Rica and shows how certain molluscs tend to prefer pools to other littoral areas and Abbott (1958) comments that in the upper ironshore of Grand Cayman, *Puperita pupa* and *Littorina mespillum* were most common in "spash pools". The West End rocks on Little Cayman contained similar "spash pools" where the hermit crab, *Clibanarius tricolor* became very abundant, as did the goby *Bathygobius soporator*. Around Little Cayman other molluscan species were found in rock pools including *Litiopa melanostoma, Tegula excavata, Echininus nodulosus, Nodilittorina tuberculata, Littorina ziczac, Acmaea antillarum* and the nerites, *Nerita versicolor, N. tessellata* and *N. peloronta*. In low water pools the echinoids *Echinometra lucunter* and *Diadema antillarum* were present; the former being recorded in pools of the inshore rocky areas of Florida Keys by McPherson (1969).

Apart from the molluscan collections by Salisbury (1953) and Abbott (1958) very little has been done to the littoral fauna of the Cayman Islands and nothing has been published specific to Little Cayman. The neglect of the littoral region is not justified as it offers a varied and diverse habitat in which many species live. Around the island the differing degrees of exposure have an effect upon the species present, their morphology and upon their vertical range in the littoral zone.

Summary

(1) The littoral rocks of Little Cayman have been examined at different sites around the Island representing different degrees of exposure.

(2) A species list has been compiled and the size distribution of the common littoral molluscs indicates that despite local variability exposure has an effect upon the mean size for any one site. In general the greater the exposure of the site the smaller the shell size although in some species the reverse is true. Some species exhibit a greater size range around the atoll than is recorded in the zoo-geographical literature.

(3) The vertical zonation of molluscs is affected by the exposure, thus on a more exposed shore or part of a shore the vertical range is often extended.

Acknowledgements

I should like to acknowledge the financial and other support given by the Royal Society and Cayman Island Government without which it would not have been possible to carry out the present survey. I should also like to thank Dr M. E. C. Giglioli and various members of his staff at the Mosquito Research and Control Unit who helped in many ways, and in particular George Giglioli and Eugene Parsons for valuable field assistance. Dr K. George of the School of Maritime Studies, Plymouth kindly prepared the tidal data from which Figure 11 was prepared. Miss Ailsa Clark identified the echinoderms collected from Little Cayman, Dr C. den Hartog the marine angiosperms and Mr R. C. Swinfen helped sorting the specimens after their return to the Plymouth Laboratory. I should like to thank the Director of the Marine Biological Association, Professor E. J. Denton, for permission to join the expedition.

References

Abbott, R.T. 1954. Review of the Atlantic periwinkles, *Nodilittorina, Echininus* and *Tectarius*. *Proc. U.S. natn. Mus.* 103, 449-464.

Abbott, R.T. 1958. The marine mollusks of Grand Cayman Island, British West Indies. *Monogr. Acad. nat. Sci., Philadelphia,* 11, 138pp.

Arnow, L., St. Clair, F. and Arnow, T. 1963. The mollusca of a lagoonal area at Playa de Vega Baja, Puerto Rico. *Caribb. J. Sci.* 3, 163-172.

Bakus, G.J. 1968. Zonation in marine gastropods of Costa Rica and species diversity. *Veliger,* 10, 207-211.

Bakus, G.J. 1975. Marine zonation and ecology of Cocos Island, off central America. *Atoll Res. Bul.* 179, 1-8.

Borkowski, T.V. 1971. Reproduction and reproductive periodicities of South Floridian Littorinidea (Gastropoda: Prosobranchia). *Bull. mar. Sci. Gulf Caribb.* 21, 826-840.

Borkowski, T.V. and Borkowski, M.R. 1969. The *Littorina ziczac* species complex. *Veliger,* 11, 408-414.

Chace, F.A. Jr and Hobbs, H.H. Jr 1969. The freshwater and terrestrial decapod crustaceans of the West Indies with special reference to Dominica. *U.S. nat. mus. Bull.* 292, 1-243.

Chapman, V.J. 1961-1963. The marine algae of Jamaica, pt.1 Myxophyceae and Chlorophyceae. Pt.2 Phaeophyceae and Rhodophyceae. *Bull. Inst. Jamaica,* Sci. Ser.

Coomans, H.E. 1958. A survey of the littoral gastropoda of the Netherlands Antilles and other Caribbean Islands. *Uitg. natuurw. StudKring Suriname,* 17 (*Stud. Fauna Curacao,* 8), 42-111.

Doran, E. 1954. Land forms of Grand Cayman Island, British West Indies. *Texas J. Sci.,* 6, 360-377.

Fraenkel, G. 1968. The heat resistance of intertidal snails at Bimini, Bahamas; Ocean Springs, Mississippi; and Woods Hole, Massachusetts. *Physiol. Zool.,* 41, 1-13.

Ginsburg, R.N. 1953. Intertidal erosion of the Florida Keys. *Bull. mar. Sci. Gulf Caribb.* 3, 55-69.

Gosline, W.A. 1965. Vertical zonation of inshore fishes in the upper water layers of the Hawaiian Islands. *Ecology,* 46, 823-831.

Hardin, D.D. 1968. A comparative study of lethal temperatures in the limpets *Acmaea scabra* and *Acmaea digitalis*. *Veliger,* 11, 83-87.

Hartog, C. den 1970. *The sea-grasses of the World.* Amsterdam: North Holland Publishing Co. 275pp.

Houbrick, J.R. 1968. A survey of the littoral marine mollusks of the Caribbean coast of Costa Rica. *Veliger,* 11, 4-23.

Idyll, C.P. 1966. Ironshore. *Sea Front.* 12, 328-339.

Lewis, J.B. 1960. The fauna of rocky shores of Barbados, West Indies. *Can. J. Zool.* 38, 391-435.

Lewis, J.B. 1963. Environmental and tissue temperatures of some tropical intertidal marine animals. *Biol. Bull. mar. biol. Lab., Woods Hole,* 124, 277-284.

Manning, R.B. 1968. A revision of the family Squillidae (Crustacea, Stomatopoda) with descriptions of 8 new genera. *Bull. mar. Sci. Gulf Caribb.* 18, 105-142.

Matley, C.A. 1926. The geology of the Cayman Islands (British West Indies) and their relation to the Bartlett trough. *Q.J. geol. Soc. Lond.* 82, 352-386.

McPherson, B.F. 1969. Studies on the biology of the tropical sea urchins, *Echinometra lucunter* and *Echinometra viridis*. *Bull. mar. Sci. Gulf Caribb.* 19, 194-213.

Morris, P.A. 1973. A field guide to shells of the Atlantic and Gulf Coasts *and the West Indies*. 3rd Edition Boston: Houghton Mifflin Co. 330pp.

North, W.J. 1954. Size distribution, erosive activity and gross metabolic efficiency of the marine intertidal snails *Littorina planaxis* and *L. scutulata*. *Biol. Bull. mar. Biol. Lab., Woods Hole,* 106, 185-198.

Paine, R.T. 1966. Food web complexity and species diversity. *Am. Nat.* 100, 65-75.

Provenzano, A.J. 1959. The shallow-water hermit crabs of Florida. *Bull. mar. Sci. Gulf Caribb.* 9, 349-420.

Rosewater, J. 1963. Resistance to desiccation in dormancy by *Tectarius muricatus*. *Nautilus,* 76, 112.

Russell, H.D. 1941. The recent mollusks of the family Neritidae of the Western Atlantic. *Bull. Mus. comp. Zool. Harv.* 88, 347-404.

Salisbury, A.E. 1953. Mollusca of the University of Oxford Expedition to the Cayman Islands, 1938. *Proc. malac. Soc. Lond.* 30, 39-54.

Southward, A.J. 1958. The zonation of plants and animals on rocky seashores. *Biol. Rev.* 33, 137-177.

Stephenson, T.A. and Stephenson, A. 1950. Life between tide-marks in North America. I. The Florida Keys. *J. Ecol.* 38, 354-402.

Stephenson, T.A. and Stephenson, A. 1952. Life between tide-marks in North America. II. Northern Florida and the Carolinas. *J. Ecol.* 40, 1-49.

Vermeij, G.J. 1973. West Indian molluscan communities in the rocky intertidal zone: a morphological approach. *Bull. mar. Sci. Gulf Caribb.* 23, 351-386.

Voss, G.L. and Voss, N.A. 1955. An ecological survey of Soldier Key, Biscayne Bay, Florida. *Bull. mar. Sci. Gulf Caribb.* 5, 203-229.

Voss, G.L. and Voss, N.A. 1960. An ecological survey of the marine invertebrates of Bimini, Bahamas, with a consideration of their zoogeographic relationships. *Bull. mar. Sci. Gulf Caribb.* 10, 96-116.

Warmke, G.L. and Abbott, R.T. 1961. *Caribbean seashells.* Narberth, Pennsylvania: Livingston Publishing Co. 346pp.

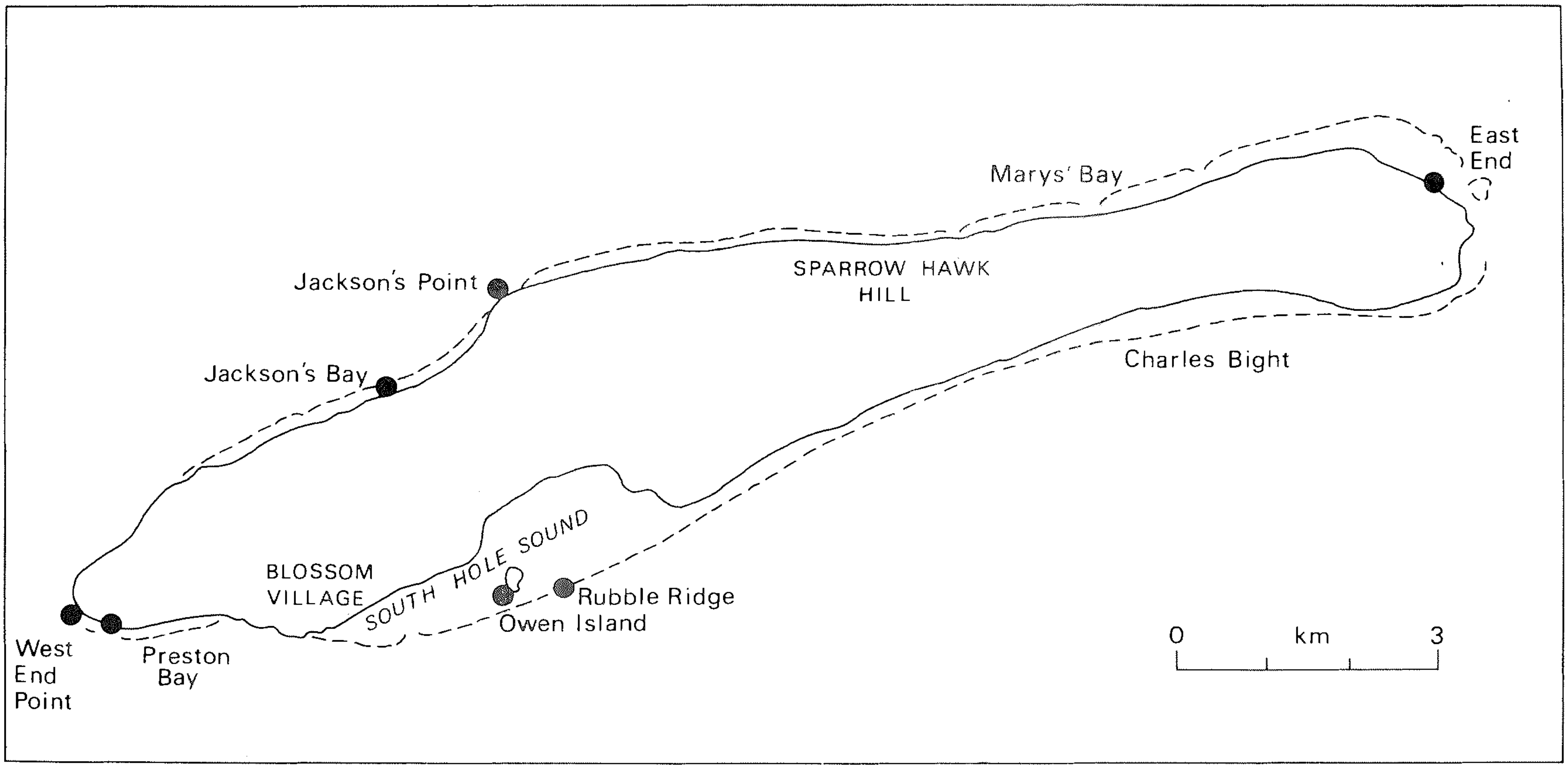

Figure 11. Map of Little Cayman showing the main coastal sampling areas

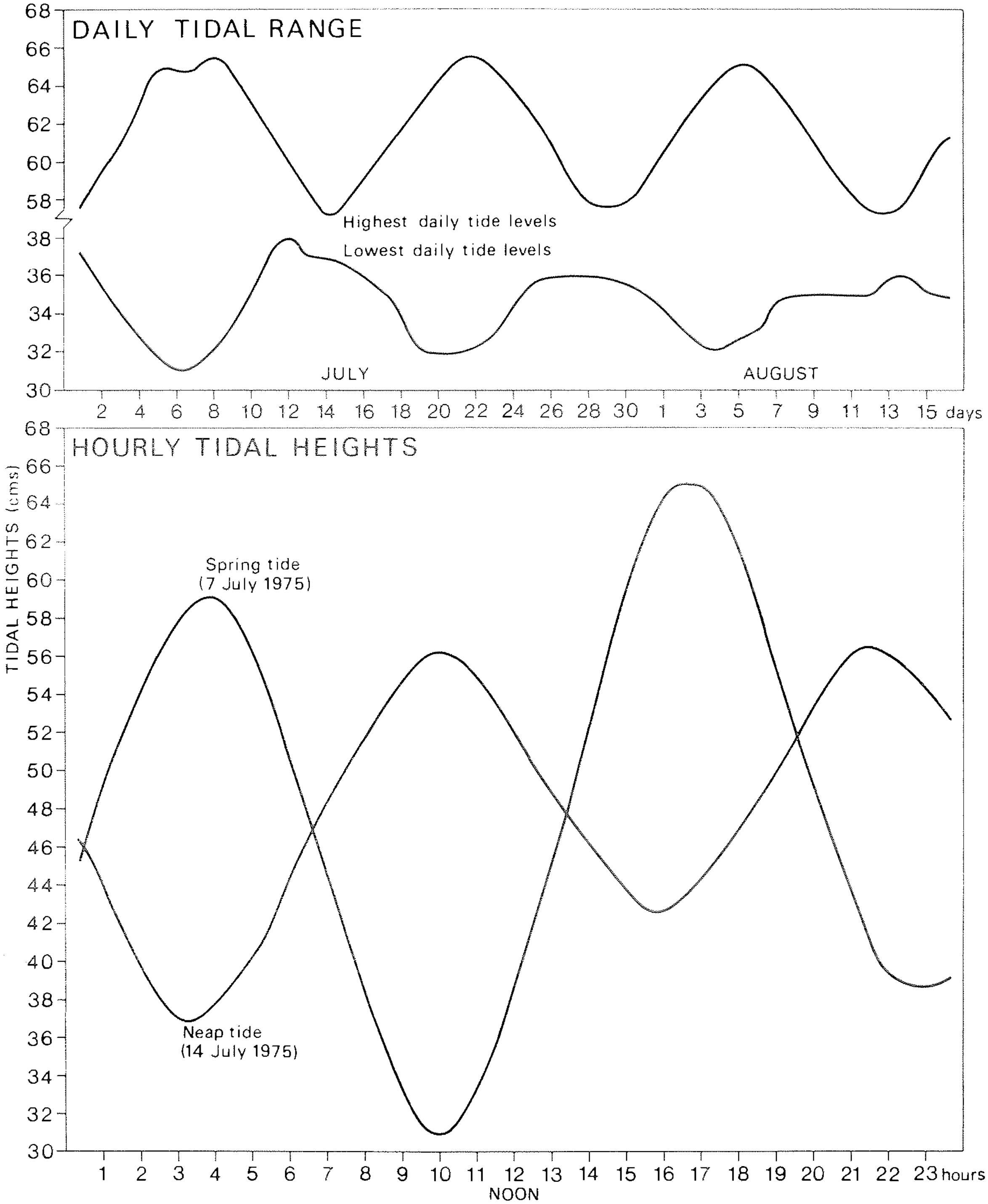

Figure 12. Graphs of the daily tidal range during the period of the expedition together with hourly tidal heights on a neap tide and a spring tide. The data were provided by Dr. K. George and based on figures obtained from *Admiralty Tide Tables*, Vol. II, 1975

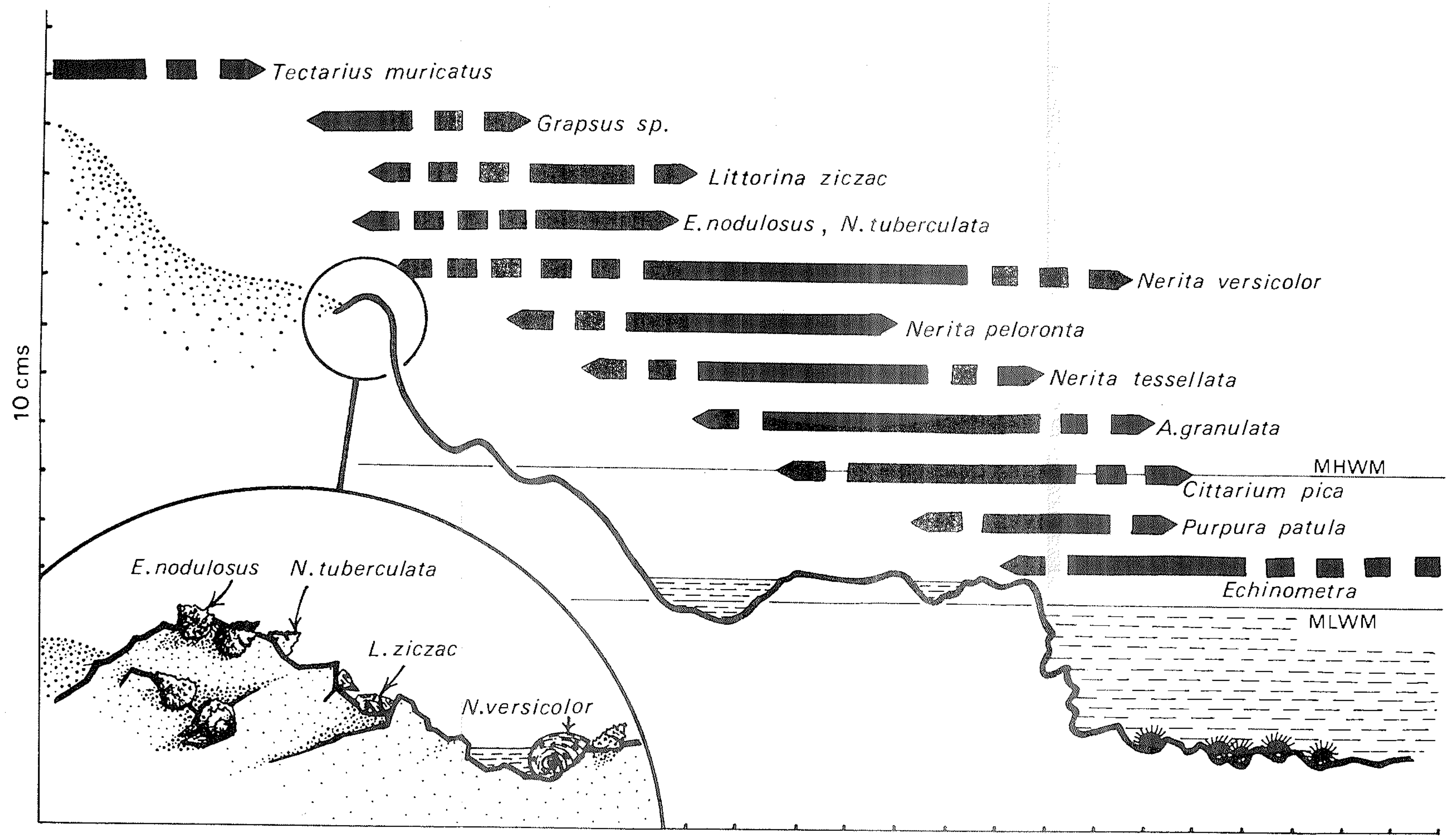

Figure 13. Profile of the shore at Preston Bay with an indication of the vertical zonation of the littoral species. The inset shows how on the upper shore some species remain in pools (*Nerita versicolor*), in moist crevices (*Littorina ziczac*), and on the open rock (*Echininus nodulosus* and *Nodilittorina tuberculata*), *Littorina ziczac* refers to the appropriate species of the *L. ziczac* "complex" (Borkowski and Borkowski, 1969) found in an area, and does so in subsequent figures

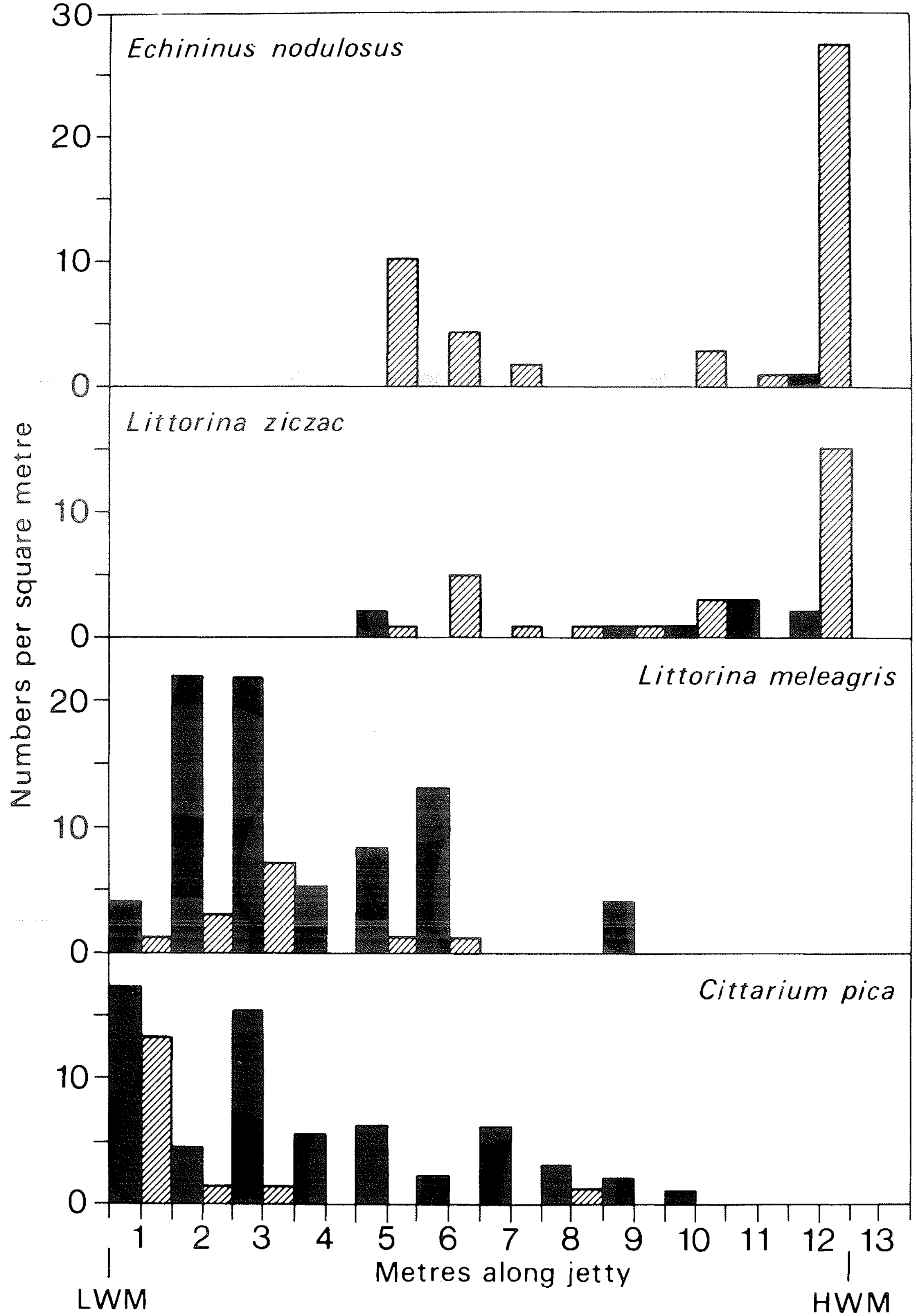

Figure 14. Histograms indicating the distribution of four species of gastropod along the jetty at Preston Bay. Black columns represent the east side of the jetty and stippled columns the west side

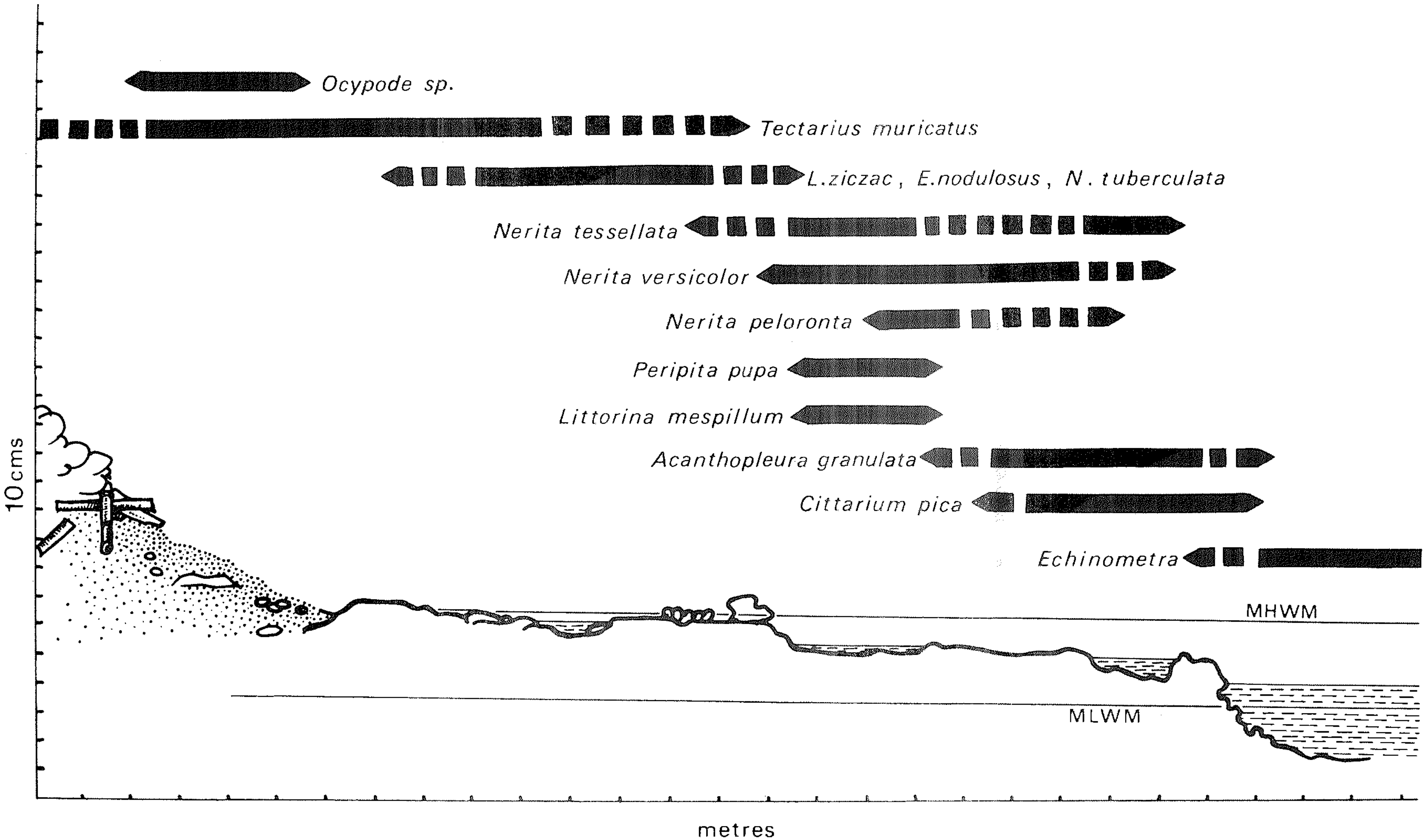

Figure 15. Profile of the shore at West End Rocks with an indication of the vertical zonation of the common littoral species

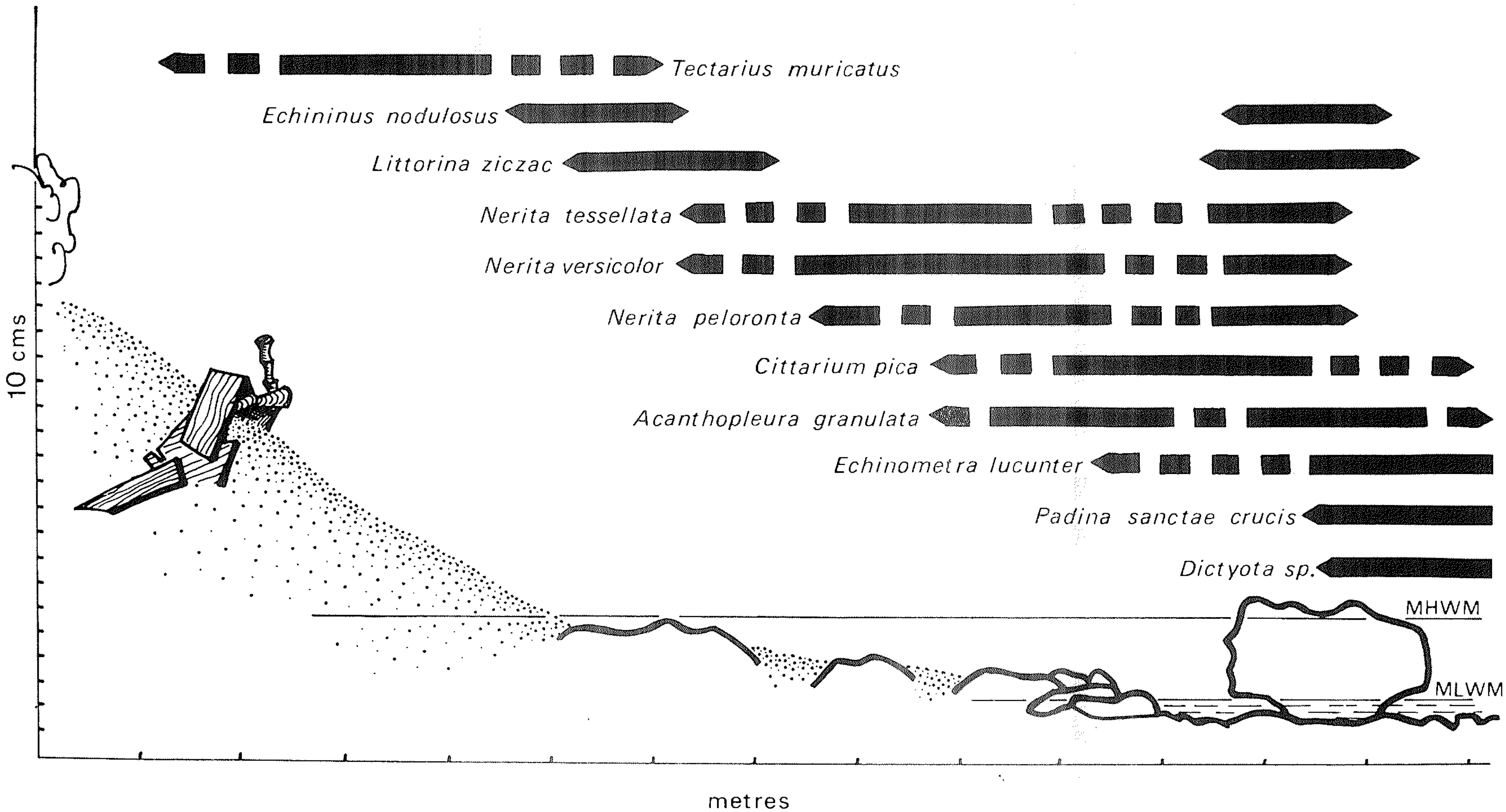

Figure 16. Profile of the shore at Jackson's Bay Point indicating the vertical zonation of the common littoral species. The double occurrence of some littorinids and nerites is a result of their presence on a large boulder found just below MLWM

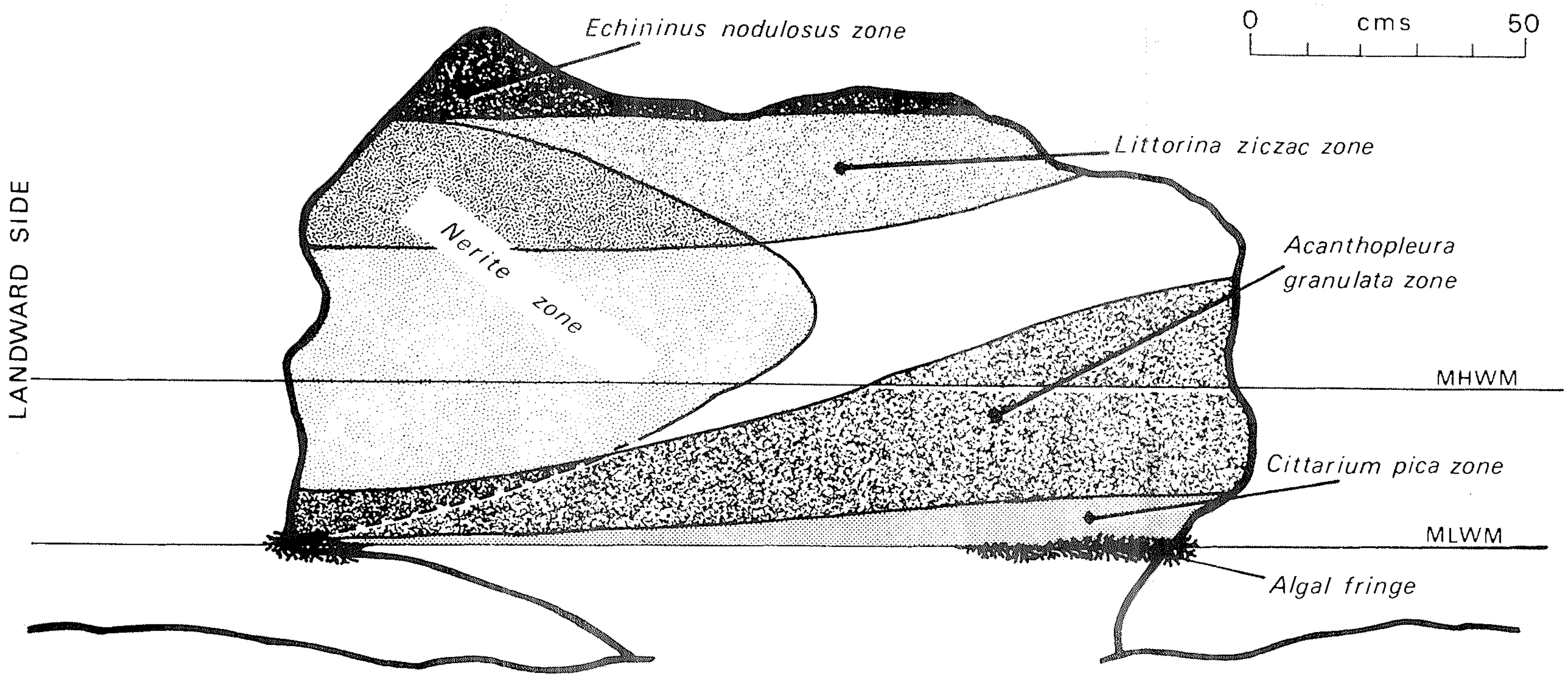

Figure 17. The distribution of molluscan zones around a boulder at Jackson's Bay Point (see Figure 16). It should be noticed that there is a difference in the extent of the zones on the seaward and landward sides of the boulder

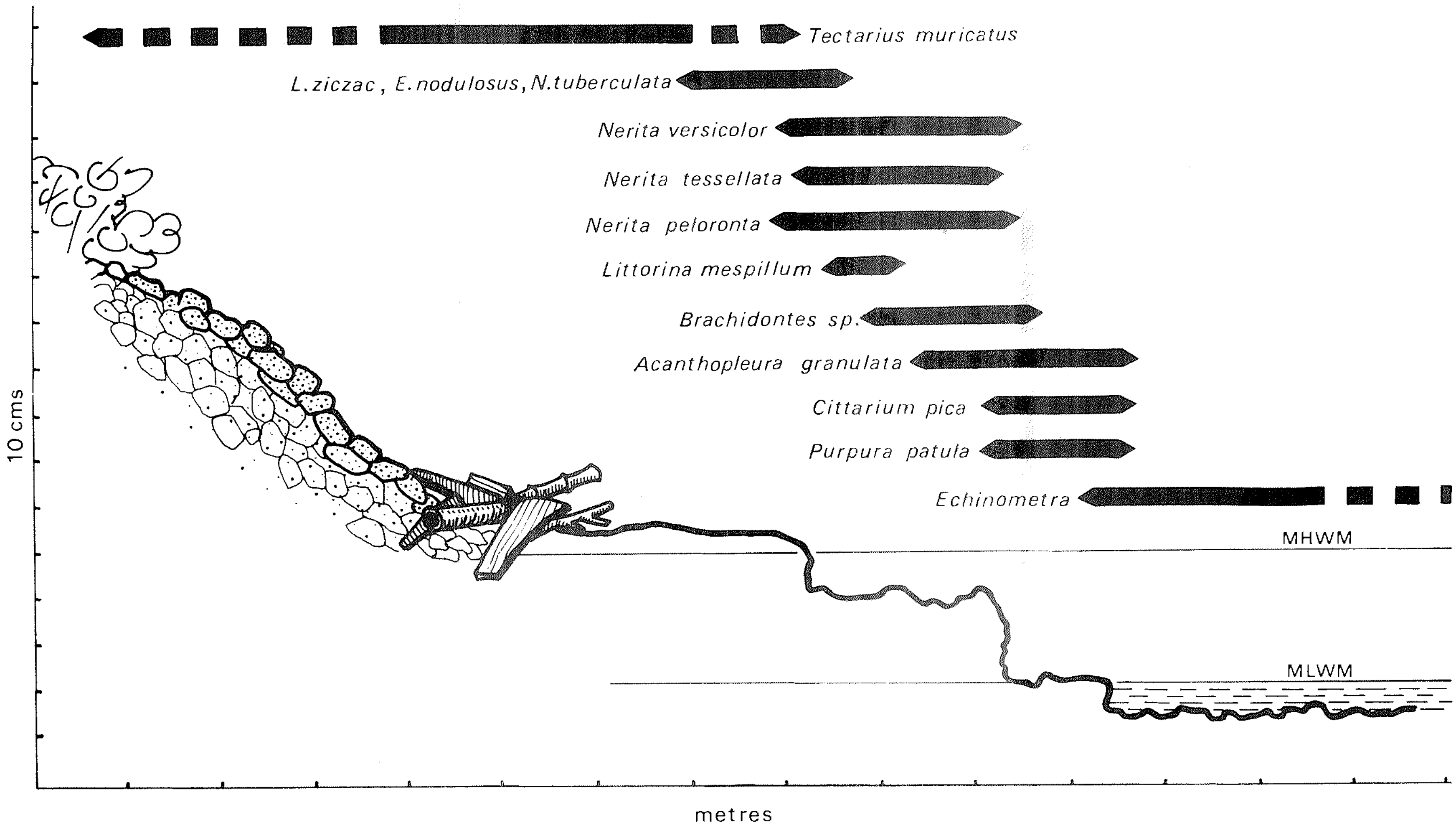

Figure 18. Profile of the shore at the East End indicating the distribution of the common littoral species

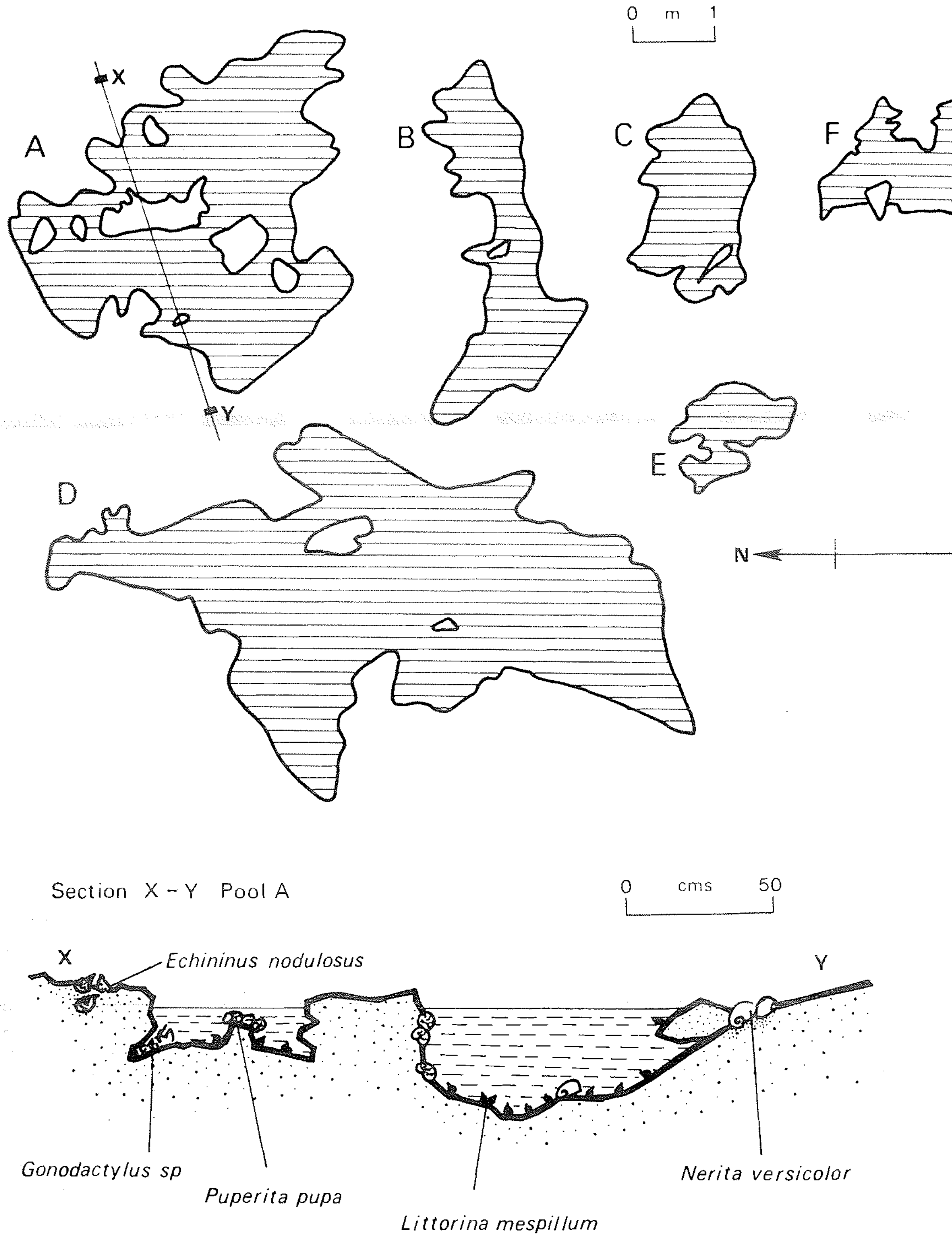

Figure 19. Outlines and orientations of littoral rock pools at West End Rocks and Jackson's Bay. Pools A, B and C occurred at approximately mid-tide levels and D, E and F at low tide levels. A diagrammatic section X-Y of pool A is given with the distribution of some of the common rock pool invertebrates

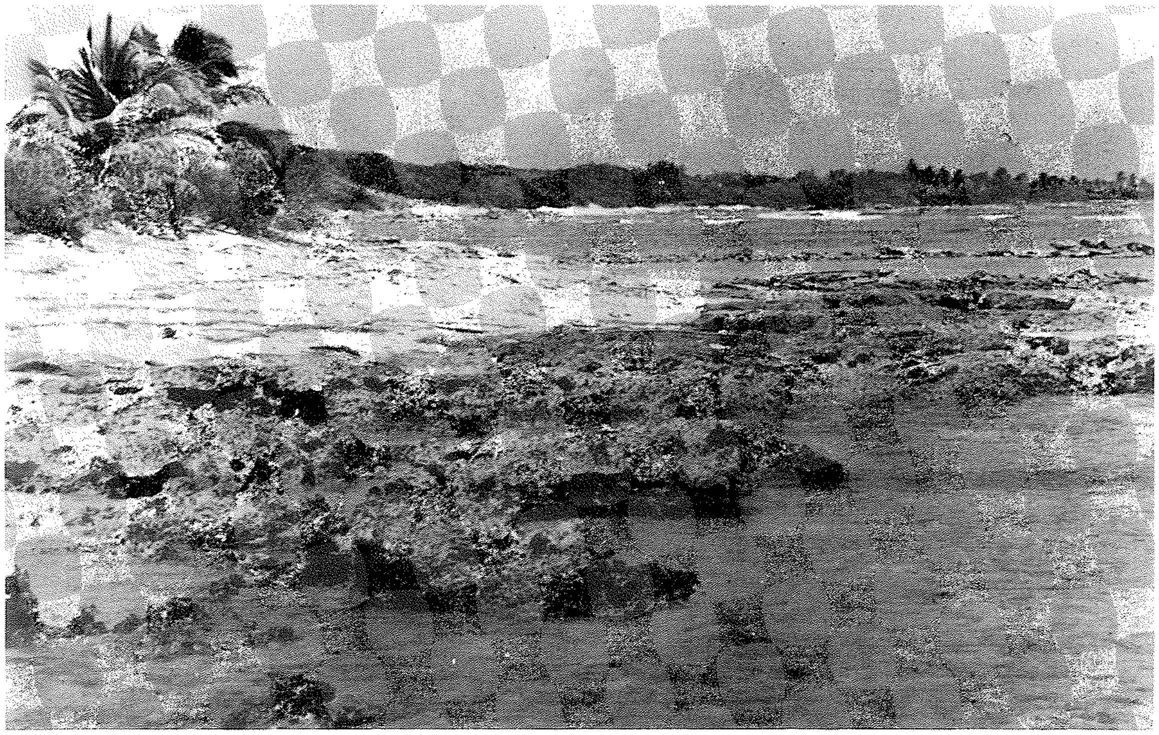

Plate 22. Preston Bay showing the exposed littoral rocks and sand beach above them

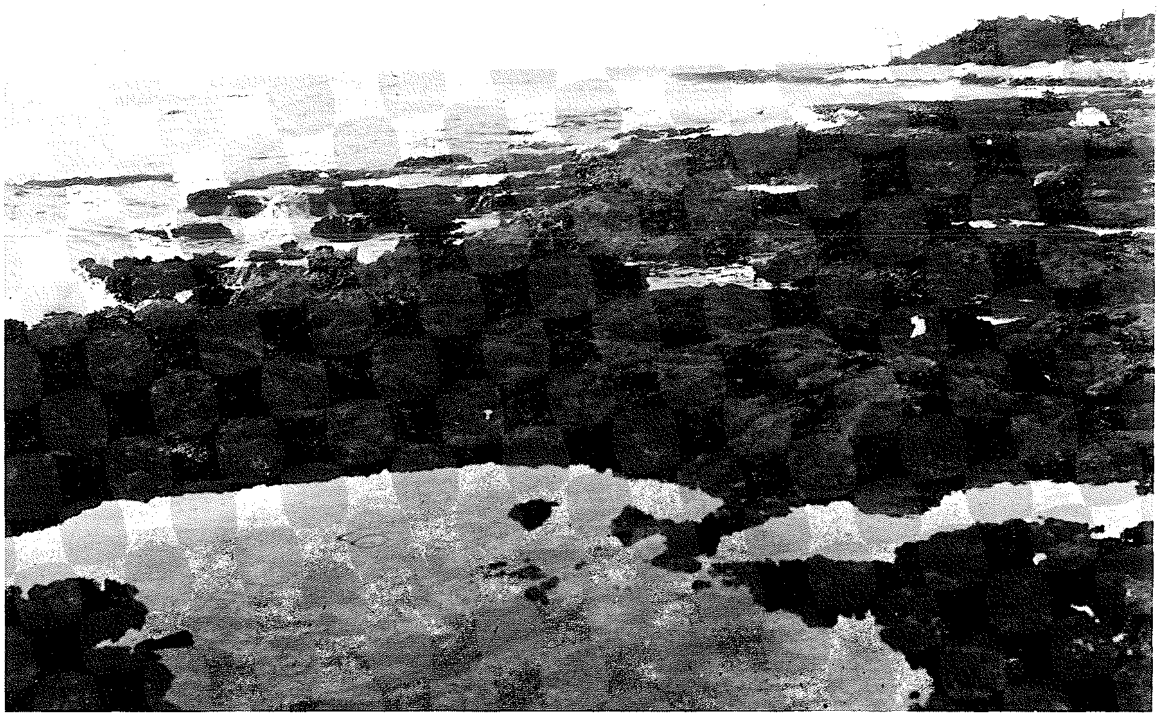

Plate 23. West End Rocks with a large littoral rock pool in the foreground

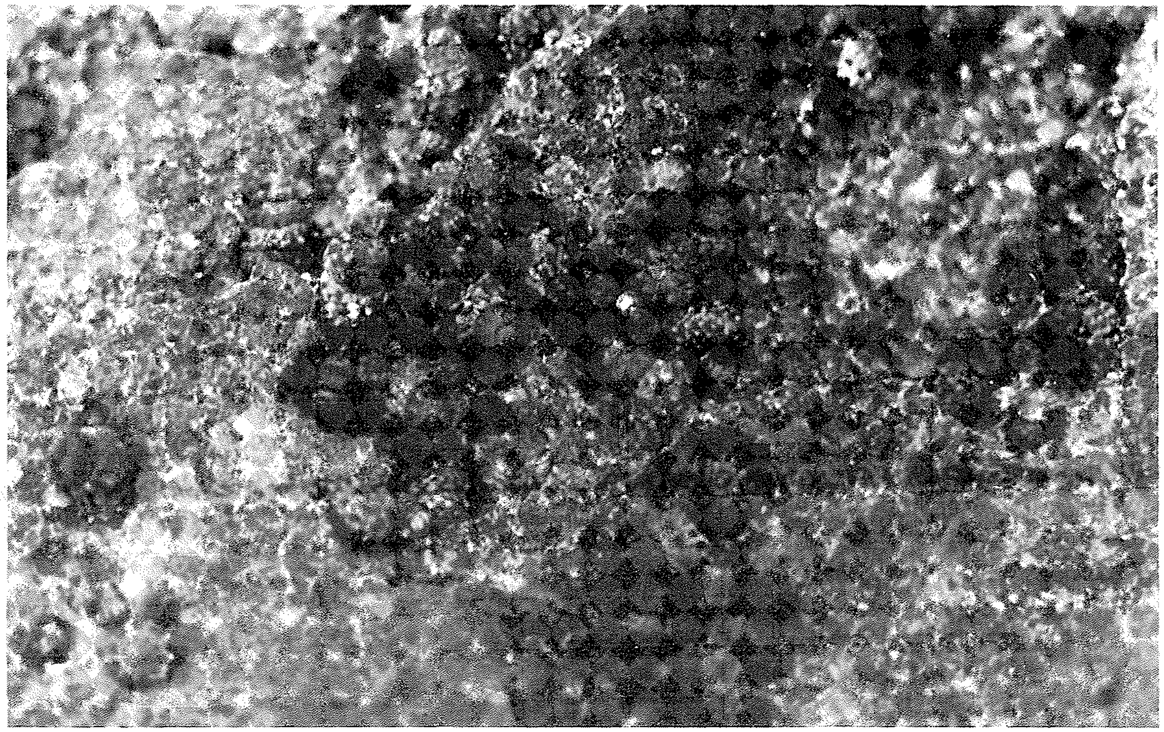

Plate 24. *Echininus modulosus* in crevices with *Littorina ziczac* on the upper midlittoral region of Preston Bay

Plate 25. *Tectarius muricatus* (arrowed) among the leaves of *Sesuvium portulacastrum* at West End Rocks

Plate 26. *Nerita peloronta* and *N. tessellata* on rocks at the midlittoral zone. *Echininus nodulosus* and *Littorina ziczac* are present in crevices

Plate 27. *Turbinaria turbinata, Padina sanctae-crucis* and *Dictyota* sp. in the lower midlittoral zone at West End Rocks

Plate 28. East End showing the steep and deeply dissected littoral region

Plate 29. The rubble ridge of South Hole Sound looking east. In the foreground is a small plant of the black mangrove *Avicennia germinans*

Plate 30. *Cittarium pica* on the jetty at Preston Bay

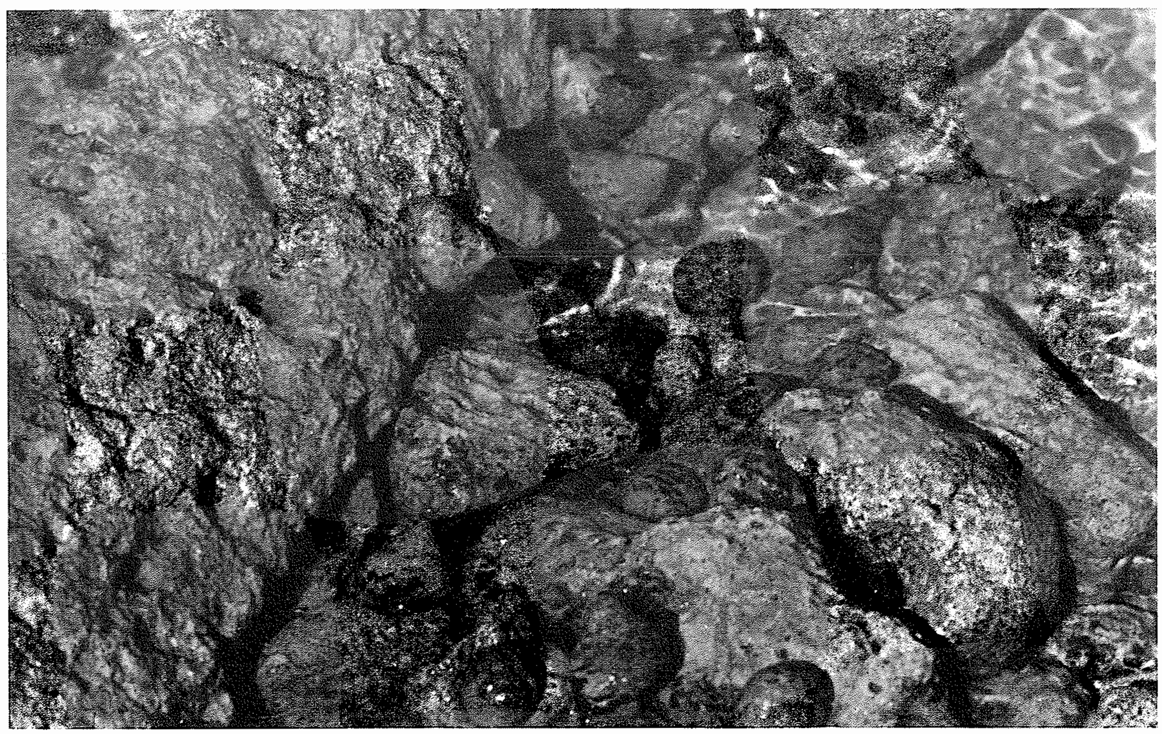

Plate 31. *Cittarium pica* covered in calcareous algae on the rubble ridge, South Hole Sound

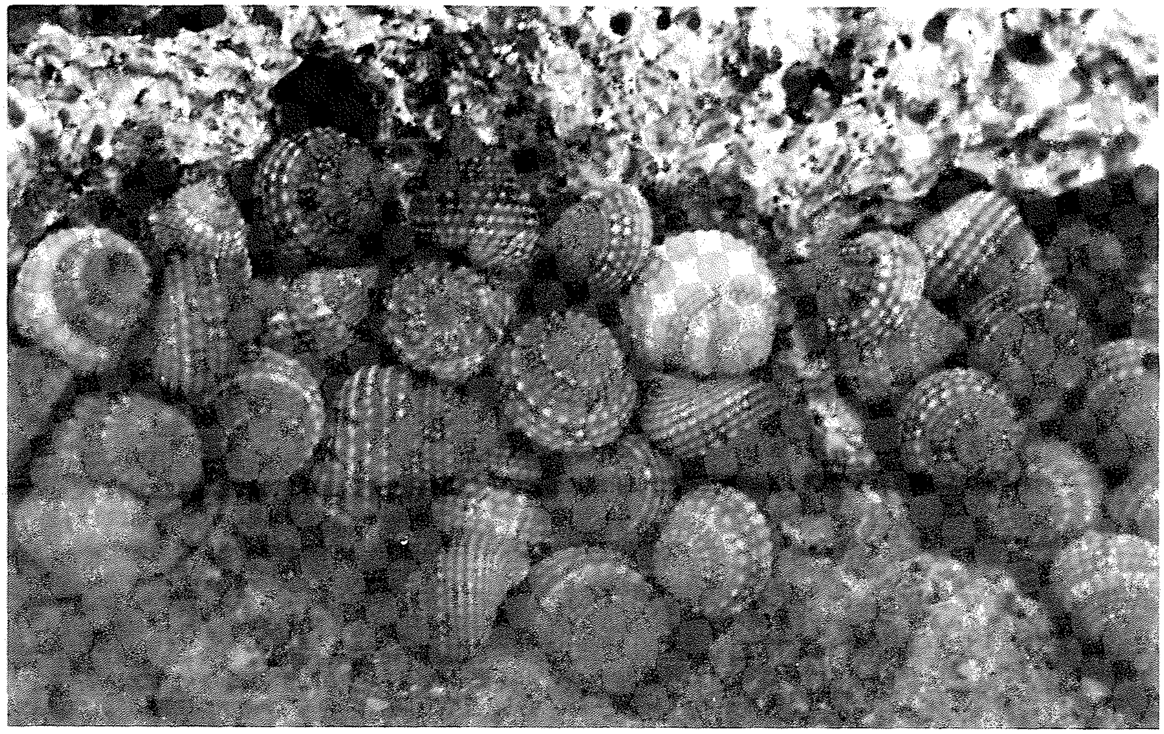

Plate 32. *Tectarius muricatus* in large numbers in the supralittoral fringe at East End

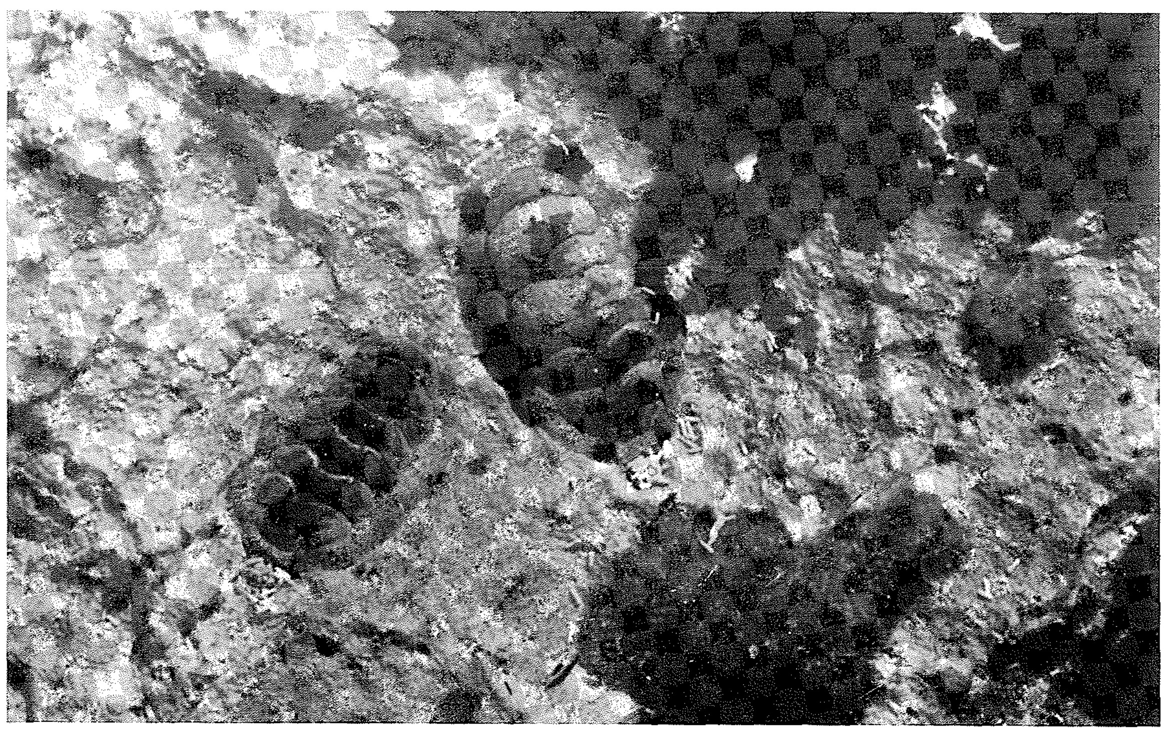

Plate 33. *Acanthopleura granulata* in shallow rock pools in the lower midlittoral zone

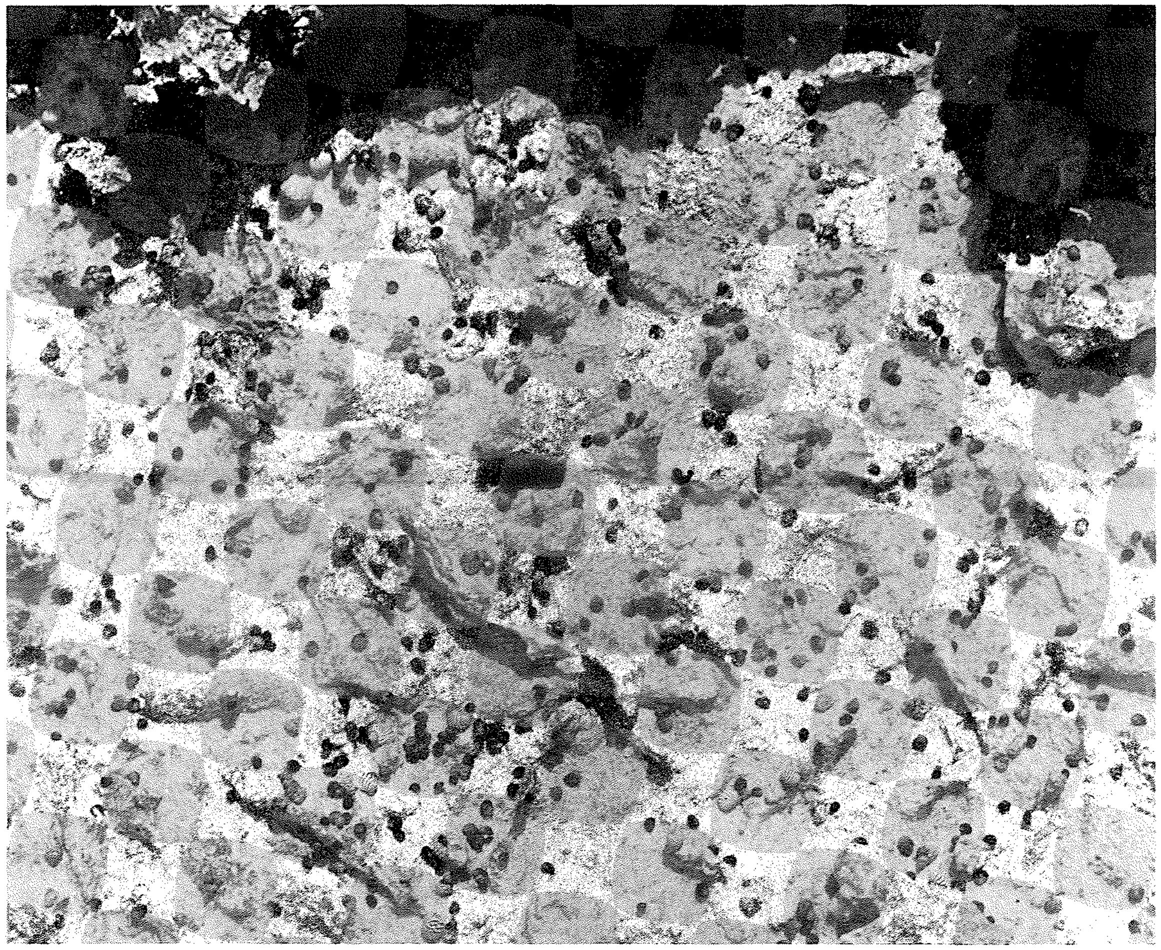

Plate 34. Rock pool at West End Rocks showing *Puperita pupa* and *Littorina mespillum* scattered over the bottom of the pool

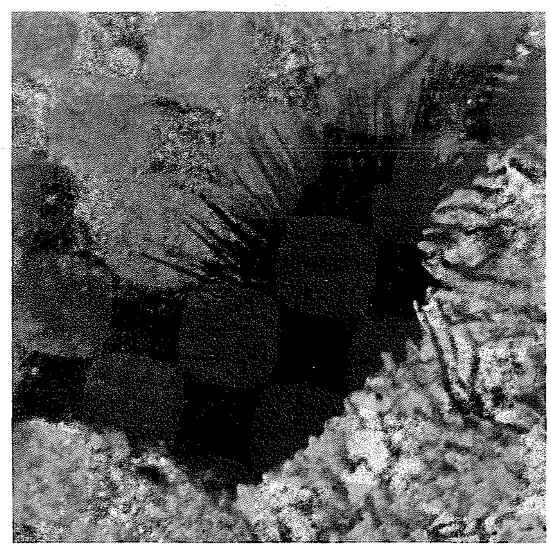

Plate 35. *Puperita pupa* gathered on a rocky pinnacle within a rock pool

Plate 36. *Diadema antillarum* in a low tide level rock pool at Preston Bay