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THE FAUNA AND FLORA OF SAND FLATS AT INHACA
ISLAND, MOÇAMBIQUE

By W. MACNAE AND MARGARET KALK

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This paper describes the distribution and certain aspects of the ecology of plants and animals on the intertidal flats around the island of Inhaca at the entrance to the Bay of Lourenço Marques, Moçambique. The flats are extensive and for the most part are meadows of tropical marine angiosperms or 'sea grasses', which have been listed by Cohen (1939). Apart from brief descriptions of the meadows of 'sea grasses' in Madagascar (Poisson 1949) and of those at Inhaca (Macnae & Kalk 1958) so far as the authors are aware this is the first detailed and comparative study of such meadows in the Indo-west-Pacific region. Variations in plant and animal communities in relation to degrees of shelter and insolation are discussed. Although mangrove swamps are also extensively developed on Inhaca shores, consideration of them has been omitted here and they will form the subject of a further paper (Macnae & Kalk 1962). All the shores of the island have been studied during periodic visits since 1952 and faunal and floral lists have been given fully in a previous publication (Macnae & Kalk 1958).

The island lies outside the tropics, but from the authors' knowledge of tropical shores of northern Moçambique (Kalk 1959) and Madagascar it is clear that the fauna

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and flora are distinctly tropical, and there are few organisms in common with the flats of South African bays and estuaries a comparatively short distance to the southward, of which descriptions have been published by zoologists from the University of Cape Town under the leadership of Professor J. H. Day.

PHYSICAL CONDITIONS

Inhaca island (lat. 26° S, long. 33° E) is virtually the isolated northerly tip of the peninsula which separates the Bay of Lourenço Marques from the Indian Ocean. Its position in relation to the bay is shown in Fig. 1. The bay is about 30 km broad and receives on its western margin the estuaries of five rivers which do not dry up in winter. The bay is widely open to the north, its eastern waters around the shores of Inhaca are under strong marine influence, and there is little trace of fresh water or of estuarine influences.

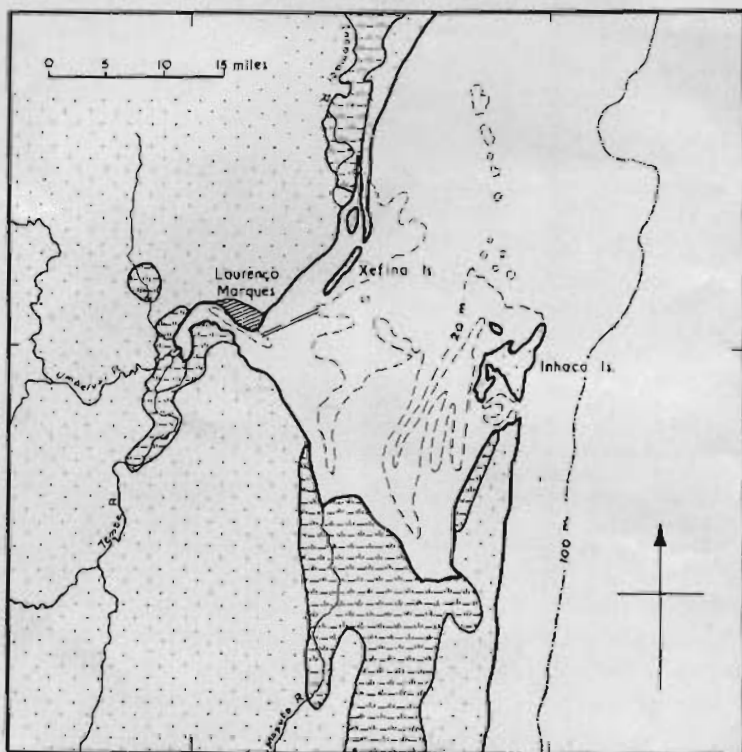


FIG. 1. Map of the Bay of Lourenço Marques.

The island, of which the greater length is 11 km and the greatest breadth 6 km, is built mainly of two long north-south ridges of sand dunes clothed with forest and other vegetation, and forming the eastern and western coastlines. There are also several lower ridges, the slacks between which are filled with freshwater swamps. From Fig. 2 it will be noticed that the northern and southern shores of the island are deeply indented bays with very extensive intertidal flats. Tidal channels pass through these flats and communicate with the ocean through breaks in the sand bars both to the north and to the south of the island. Such a channel separates the island from the mainland peninsula to the south. Tidal currents in these channels are strong at most states of the tide but at extreme low water of springs the channels are in some places shallow enough to cross on foot.

Climate

At 26° S latitude, the island lies in the region of transition from tropical to warm temperate climate, and within an area of hot wetter summers and warm drier winters. The mean annual air temperature (recorded on the west side) is 22.8° C with a mean annual range between 18.7 and 26.9° C. Rain may fall at any time of the year, but it is not often very heavy even in summer. Winds are comparatively gentle and are usually

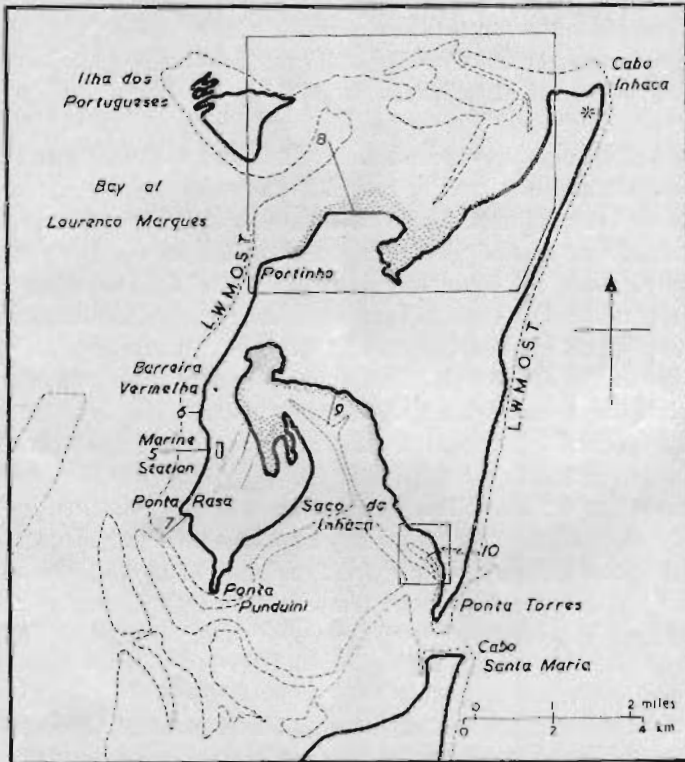


FIG. 2. Map of Inhaca island. Mangrove swamps are stippled. The upper inset will be found enlarged as Fig. 3. The lower inset will be found enlarged as Fig. 4. The numbered lines show the location of the transects shown in Fig. 5.

either from the east or from the south; local conditions appear to over-ride the southeasterly trade winds. Occasionally the south wind reaches gale force but seldom for more than a few hours. Humidity averages 77% and evaporation is high during the day. The detailed climatic factors affecting the shores of the island are determined by two special features superimposed on those which might be expected at this latitude. These are the Moçambique current and the shallow waters of the Bay of Lourenço Marques.

Sea temperature

Throughout the year warm waters of the South Equatorial Current flow westward across the Indian Ocean to impinge on the coast of Africa to the north of Madagascar. Most of this water is deflected into the Moçambique channel where the width is narrowed and the velocity increased. At the latitude of Inhaca it flows some 10 miles out to sea. Between

this strongly flowing current and the shore a northward flowing counter current brings cooler water close inshore. It is this counter current which has induced the formation of Inhaca island and the adjacent peninsula. These currents vary in strength from year to year and from month to month. In some years the Moçambique current comes close inshore and then the Bay of Lourenço Marques receives a supply of warmer water.

The waters of the Moçambique current are of high temperature and high salinity. Measurements of surface water temperatures taken by the R.R.S. DISCOVERY II in April 1935 showed that from latitude 21° to 28° S in the middle of the Moçambique Channel, there was a drop in temperature only from 26.58° to 25.18° C. At midnight in midwinter, surface temperatures of between 23° and 24° C were recorded by the R.R.S. WILLIAM SCORESBY between latitudes 20° and 21° S and the air temperature was a fraction lower.

Unfortunately sea temperatures at Inhaca have not been recorded with any regularity; attempts have been made, however, to correlate daily temperature variations in intertidal water with air temperatures. These observations indicate that except in July the water temperature is for most of the day higher than that of the air. The range on the west coast flats is between 18° C on July mornings to 24° C in the early afternoon. In December the daily range is between 23° and 31° C. In more sheltered areas the pools may reach 37° C. These figures indicate the tropical nature of the temperature of the inshore waters, at least on the intertidal flats. These are exposed to the force of the sun's rays during spring tides, and since such tides are lowest towards mid-day, the shallow water over the flats is considerably warmed. Records of temperature have been taken simultaneously on the flats opposite the station on the west shore and in one of the warmer coves near the mouth of the Saco. This series of observations indicated that the shallow water standing on the flats in these coves may be warmed to a temperature as much as 6° C above similar pools off the laboratory. On the other hand, after the turn of the tide the water in the cove dropped to a lower temperature since the tidal currents bringing in oceanic water reach it sooner.

Tides

The pattern of tides along the east coast of Africa is semi-diurnal. According to the Tabela de Marés, published annually at Lourenço Marques, the amplitude of extreme spring tides is 3.7 m and that of average springs 3.3 m. The average neap tidal range is 1.5 m. The low tide mark of the smallest neap tide approximates to mean tidal level. As a result of a sharp change in configuration of the shore just above this level the sea during neap days appears to recede hardly at all. It seems to be stationary for 3 hours at high tide and again at low tide with a horizontal distance of scarcely 50 m between. A great contrast is seen during spring tides when up to 700 m of flats are uncovered on the west shores and over 4 km on the southern and northern shores.

Salinity

The nearest river mouth is over 30 km distant, and the water of the bay is mixed with tidal currents from the Indian Ocean of which the salinity is 35.47‰. The island has no true river but there is seepage of fresh water through the dunes to the shores. Wells yielding fresh water at a depth of 4 or 5 m have been dug near the Marine Station. The level of freshwater seepage close to the base of the steep upper shore on sandy beaches is indicated by a green band of *Convoluta macnaei* E. du B. Marcus. The shores of the northern bay and of the Saco have mangroves at a comparable level.

The salinity of the intertidal water over the flats on the west shore varies between 30.0 and 33.9‰. In the mangroves some values were as low as 12‰ in drainage pools and as high as 42‰ in pools drying out on the flats near high water mark.

THE INTERTIDAL FAUNA

The intertidal flats along the sheltered shores of the island of Inhaca follow one of two distinct patterns. At most places on the west coastline of Inhaca, on the sheltered shores of the Ilha dos Portugueses and of many of the coves towards the entrance of the Saco da Inhaca near Ponta Torres there is a steep upper shore, extending from just above high water mark down to mean sea level, below which the lower shore slopes very gently down to the edge of the channel; there is, therefore, on these shores a very sharp change in the form of the slope (Figs. 5-7, 10). In more sheltered areas, towards and at the head of the Saco da Inhaca and on the southern shores of the northern bay the slope is gradual all the way from extreme high water mark down to the edges of the several channels; in such places the upper shores are colonized by mangroves which are described elsewhere (Figs. 8, 9).

Rocks crop out at places on all shores of the island and coral debris spreads out over the lower shore near coral reefs. The flats in the immediate vicinity of the Estação de Biologia Maritima have been studied in some detail and will be compared with those elsewhere on the island. All these flats are more or less protected from wind and all are completely protected from the swell and wave action of the ocean.

Line transects were made at two localities on the west shore close to the laboratory. A numerical analysis of the fauna was made in areas of 1 m² to a depth of 20 cm, at intervals of 33 m from high to low water; coincidentally samples of the substratum were taken for mechanical analysis (see p. 123). Subsequent sampling of several areas in selected habitats on all shores of the island have confirmed the general application of the findings of these transects. In counting the animals in the selected squares the method used was one of hand picking, supplemented by sieving. The latter was found to be not very successful, for polychaetes were often missed and invariably polychaetes and the smaller enteropneusts were broken up in the sieving process.

The shores of Inhaca differ from temperate shores that have been reviewed by Raymont (1955), in that the numbers of individuals of one species, in most cases, is never very great but the number of species (in many different phyla) is exceptionally large. The data are presented, therefore, in qualitative and descriptive rather than in tabulative numerical form. Only the commonest animals are included in Figs. 5 and 6, which represent the transects drawn to scale. The positions of the two transects are indicated in Fig. 2. These transects indicate that for descriptive purposes the shores may be divided into four zones.

1. THE SUPRALITTORAL FRINGE follows one of two forms depending on the shore profile; on the west shore with moderate wave action it is dominated by ghost crabs of the genus *Ocypode*, and by talitrid amphipods; on more sheltered shores it forms the landward fringe of the mangrove swamps.

2. THE UPPER MIDLITTORAL also follows one of two facies according to the shore profile. On the western shore it is in two sections with the sudden change of slope of the beach between. The steep slope is dominated by *Donax faba* Gm. and eurydicid isopods.

The transition from the slope to the flat is in many sections of the beach marked by a green band of *Convolvula macnaei*, a species containing symbiotic green algae. Like *C. roscoffensis* in Brittany, the Inhaca species migrates vertically, being positively phototactic, and it also reacts to local vibrations by disappearing into the sand. The flat which follows is dominated by tubicolous polychaetes of which *Phyllochaetopterus elioti* Crossl. is the most numerous. Sometimes there may be a sparse growth of *Lyngbya majuscula* Harv. on the surface, but otherwise the area is bare of plants. There is a noticeable layer of silt on the surface and the substratum is firm muddy sand. Where the slope is gradual and mangroves occur they occupy, as will be shown later, parts of these two zones.

3. THE LOWER MIDLITTORAL extending from around mean low level of neaps to average low tide is an area which has large expanses of three distinct associations:

(i) where the surface of the sand is cleaner than the rest and the water table lower than is usual in this zone the crab *Dotilla fenestrata* Hilg. is dominant. The water table is usually between 10 and 15 cm from the surface;

(ii) where the substratum is muddy and the surface damper, with the water table some 1-5 cm below the surface at low water of springs, the crab *Macrophthalmus grandidieri* M.-Edw. is dominant;

(iii) where the surface area is wetter with the water table at or very close to the surface, the 'sea grass' *Diplanthera uninervis* (Forsk.) Aschers. is the most conspicuous organism; *Thalassia hemprichii* (Ehrenb.) Aschers. is occasionally co-dominant but extends downwards to the lower limits of the next sub-zone.

4. THE INFRALITTORAL FRINGE, extending from average low tide level down to extreme low water, may show two mutually exclusive facies:

(i) In emergent areas there is a zone of clear fine sand in which *Asteropecten granulatus* M. & T. is characteristic. The water table here may be as much as 20 cm below the surface at low water; locally such a sandbank may extend further upshore and usurp the lower portions of the higher zone.

(iia) The shore down to mean low water of springs is covered with fields of 'sea grasses' in which *Cymodocea serrulata* (R.Br.) Aschers. & Magnus and *C. rotundata* Aschers. & Schweinf. predominate. These plants are just covered with standing water at low tide; at exceptional low tides all the leaves which are out of water get overheated and die. The sand is of mixed constitution but tends to be finer than in the zones above. *Syringodium isoëtifolium* (Aschers.) Dandy occurs with these and extends both to higher and lower levels.

(iib) In areas which are always under water *Cymodocea ciliata* (Forsk.) Ehrenb. & Aschers. occupies circular patches which become confluent. This species has spread up from the infralittoral where it ends abruptly in the channel at a distinct line some 4 m below mean low water of springs.

Where a suitable substratum is available in the infralittoral fringe corals grow and in some places these have aggregated into small reefs. The shore may flatten out into an extensive area at any one intertidal level. This has the effect that one of the four zones may predominate at a particular locality while the others are foreshortened. Thus a different stamp is given to shores around the island.

THE SUPRALITTORAL FRINGE

The west shore

At the uppermost levels the predominant crab on the west shore is the greenish-grey *Ocypode ceratophthalmus* Pallas, but when crabs are caught in large numbers about one in thirty will be found to be the pink *O. kuhli* de Haan, a crab more typical of wave-beaten shores. Their habits are similar but *O. ceratophthalmus* prefers to forage at night. Crowds may be encountered on the lower sand flats during the night low tides, they are especially abundant in summer. Only a few juveniles appear during the day, running with incredible speed, their eye stalks not yet grown beyond their eyes. There is little indication during the day that the crabs are buried, most of them have burrowed in the sand between high neap and high spring levels. Juveniles are at a slightly lower intertidal level. After dark they emerge through spiral burrows and hundreds of hillocks appear on the slope, to disappear again when it is washed by the early morning high tide. The crabs may be found by digging to a depth of about 50 cm. At the edge of the bush just above high water mark two species of land hermit crab, *Coenobita cavipes* Stimps. and *C. rugosus* M.-Edw. are common but being secretive are rarely seen. Large individuals usually live in shells of the giant land snail *Achatina* sp. and juveniles in shells of *Nerita* spp. In the drift line of cast-up *Cymodocea* weed, the amphipod *Talorchestia malayensis* Tatt. (previously known only from a greenhouse in Singapore) and *T. australis* Brnrd. are abundant.

The Saco da Inhaca

As has already been mentioned the shore profile of the Saco da Inhaca is very different from that of the western shore. Over most of these beaches the slope is gentle downwards from extreme high water mark to the edges of the tidal channels where it becomes abruptly steeper. In the coves toward Ponta Torres the supralittoral fringe is occupied by dune rock, weathered into sharp pinnacles and irregular edges; there, the sandy slope begins at a level below that of high water of neaps and continues downwards interrupted here and there by mushroom-shaped masses of dune rock. Mangroves form quite extensive swamps at the head of the Saco and occur as a fringe over most of the shores of this bay. Shallow tidal channels, commencing in the bare areas to landward at the foot of the dunes, cross the swamp and drain into a permanent main channel which is about 1 m deep at low tide. On the lower shore the main mangrove channel peters out over the flats. Adjoining the landward edge of the mangrove swamps there are dunes covered with bush and in a few places, freshwater swamps. Between the freshwater swamps and the edge of the mangroves clumps of the fern, *Acrostichum aureum* L., are conspicuous among a sward of *Juncus kraussii* Hochst. Both these occur above the reach of all except the highest spring tides.

The level of high water mark of ordinary spring tides is normally marked by a community dominated by *Chenolea diffusa* Thunb. and *Sporobolus virginicus* (L.) Kunth., followed frequently by a narrow zone of *Juncus kraussii* and then by a mangrove of which the ecology is described elsewhere (Macnae & Kalk 1962). On some sandy beaches *Arthrocnemum perenne* (Mill.) Moss var *radicans* (Sm.) Moss. acts as a pioneer among the roots of *Avicennia* and in other localities particularly in and around areas dominated by *Uca inversa* a sward of *Arthrocnemum australasicum* (Moq.) Moss occurs with *Sesuvium portulacastrum* L. as a conspicuous associate. The latter plant often occurs in the shade of the uppermost mangroves.

THE UPPER MIDLITTORAL

The west shore

Where the shore is exposed to some wave action, the upper midlittoral is divided into two distinct zones; there is a sandy slope above a flat dominated by tubicolous polychaetes. The characteristic animal of the upper sandy slopes of the western shores of the island is *Donax faba* Gm. of which certain aspects of its habits and distribution will be discussed in a separate paper. Juveniles of two other species of wedge mussels have been found in the sandy slope, viz. *D. aemulus* Smith and *Donacilla africana* Turton. The sandy slope is otherwise almost barren. A Eurydicid isopod, *Pontogeloides latipes* Brnrd. is present and occasional small specimens of *Ceratonereis erythraeënsis* Fauv. and *Glycera subaena* Gr. have been found.

The upper levels of the flat are dominated by tubicolous polychaetes which apparently exploit the high silt value of the zone. They differ in the grades of sand utilized in the construction of their tubes. The dominant species is *Phyllochaetopterus elioti*, a blue chaetopterid, which constructs straight, narrow, tough, horny tubes 15 cm long, coated with sand of medium grade. The tubes reach down to the reduced layers of the substratum and the posterior ends are black. They end at the water table. These worms congregate in slightly damper depressions and individual tubes in the aggregations may protrude some 20 mm above the surface. At low tide no indication is given as to whether the tubes are inhabited when they are *in situ*. A density of population of between 100 and 200/m² is usual. Occasional clumps of the fragile sandy tubes of *Mesochaetopterus minutus* Potts are also present at this level and they are more abundant towards its lower limits.

Patches of cleaner-surfaced sand show holes from which radiate fine lines made by the ciliated, string-like, sticky red tentacles of the terebellid worm *Streblosoma persica* Fauvel. This worm constructs fragile tubes of coarse sand held together by solidified mucus. The sticky tentacles sweep the sand and gather up a coating of sand which is then wiped off against the mucus-coated body until a soft mucous tube impregnated with sand is made. Such a tube is much wider than the worm itself. Up to thirty were found in a square metre.

Other terebellids which may occur in this zone in smaller numbers have an optimum in the lower shore. These include, *Loimia medusa* Sav. with wide parchment-like tube varying in colour between light and dark grey according to the aeration of the environment; *Terebellides stroemi* Sars and *Pista brevibranchia* Caullery both of which have stronger sand-coated tubes. *Owenia fusiformis* D. Ch., a green worm, constructs a gelatinous tube with tapering ends, the tube is impregnated with medium or fine sand depending on the substratum in which it occurs. This worm is frequent here and extends down into the *Cymodocea* zones.

The pink sipunculid, *Siphonosoma cumanaensis* Kef. is common with a concentration of 10-20/m². A characteristic animal of the moister parts of this zone is a species of Echiuroid, which up to the present has evaded capture. Its long sticky tongue-like proboscis may be seen on the surface, and this proboscis disappears with a jerk on the slightest disturbance into a vertical burrow lined with clean sand and at least 40 cm deep.

Errant polychaetes are more abundant in the zones below low neap tide level; carnivorous species common at the upper levels under discussion include: *Glycera alba* Rathke, *G. subaena* Gr., *Nephtys tulearensis* Fauvel, *Ceratonereis costae* (Gr.) and *C. erythraeënsis* Fauvel. At the level occupied by these worm tubes and extending

downwards there is a large population of enteropneusts. *Saccoglossus inhaensis* Kapelus, constructs a permanent spiral burrow of hard cemented sand. *Balanoglossus studiosorum* v.d. Horst is abundant in sand with some inclusion of gravel and *B. hydrocephalus* v.d. Horst in softer sand with no gravel.

An animal highly characteristic of the flats appearing at this level and extending downwards to the first plant zone is the ocypodid crab *Macrophthalmus grandidieri*. This crab is confined to very damp situations and is dominant in patches of the succeeding zone.

The Saco da Inhaca and northern bay

At the head of the Saco the lowest mangrove trees extend downward into the upper parts of the midlittoral. As a result of this where mangroves are developed to their full extent, the tubicolous polychaete zone characteristic of the west shore appears to be absent. On the other hand where the mangroves do not descend to their potentially

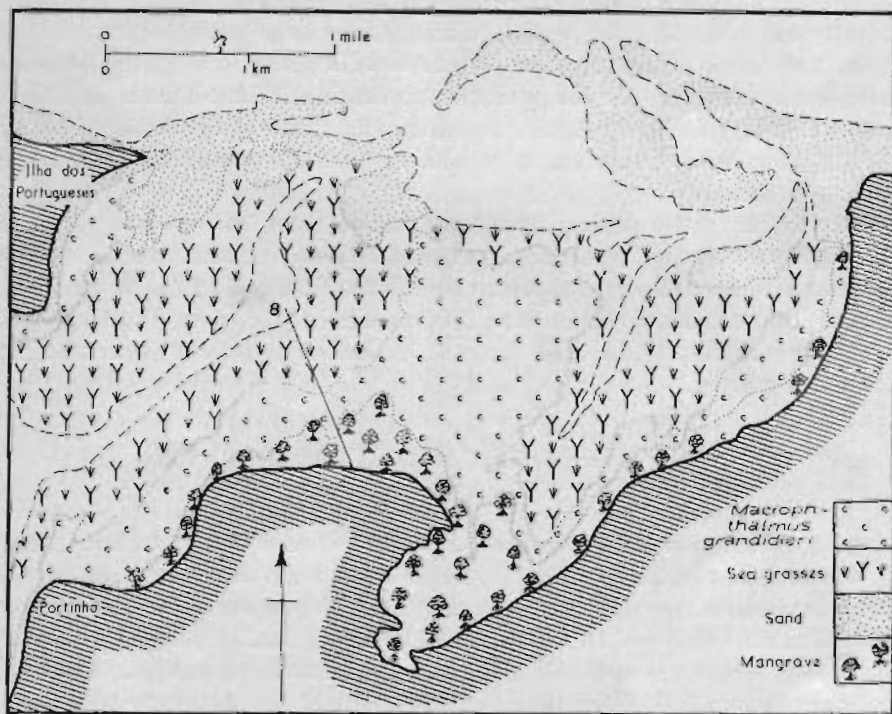


FIG. 3. The northern bay to show the distribution of intertidal communities. The numbered line indicates the location of transect shown in Fig. 5d.

lowest limit, as for example along the eastern shore of the Saco, such a zone dominated by *Phyllochaetopterus* with occasional clumps of the tubes of *Mesochaetopterus minutus* present, may be found at its characteristic level. In a few places between the scattered *Avicennia* trees there are patches of superficially clean sand which are colonized by *Dotilla fenestrata*. Such patches are at a level slightly higher than these crabs are to be found on the west coast for they are above high water of the smallest neap and about 120 cm below high water mark of spring tides; *Dotilla* patches on the west shore are

around 200 cm below high water mark. Most of the specimens of *Dotilla* seen at this high level were juveniles.

In other places the substratum below the mangrove is of a sandy mud and this is colonized by *Macrophthalmus grandidieri* and an association of animals which normally accompany it and which will be described later.

Owing to slight changes in level and in strength of the tidal currents there are among the *Macrophthalmus* associations small raised more sandy patches characteristically colonized by *Dotilla* around the edges of which are to be found a row of holes belonging to *Uca marionis* (Desm.), living here but foraging at low water over the muddy flats adjoining. In such places also the uppermost of the 'sea grasses', *Diplanthera uninervis* and *Thalassia hemprichii*, may reach almost to the lowest *Avicennia* pneumatophores. Thus this zone is also at a higher intertidal level than it is on the west shore, for at high water of the smallest neap tide at the end of September 1958, it was covered only to a depth of about 25 cm, while that on the west shore was almost 1 m under water.

By and large the upper midlittoral in the northern bay (Fig. 3) shows a very similar zonation to that in the Saco da Inhaca. In front of the large mangrove swamps there is usually no tubicolous polychaete zone. Where there is a narrow fringe of *Avicennia*, as for example along the shore of the peninsula terminating in Cabo Inhaca the tubicolous polychaete zone is typically developed. Similarly in the shores of the Ilha dos Portugueses there is a narrow *Phyllochaetopterus* zone with sparse *Diplanthera* below a steep, barren slope of coarse sand.

Into the northern bay run two main channels, one from the west and one from the east. These do not meet but overlap somewhat in the middle of the flats. The tip of each of these channels is surrounded by sand banks and these banks are fixed by very extensive colonies of *Mesochaetopterus minutus*. This animal is, therefore, in this region an important agent in binding the sand. There are few other organisms present among this mass of worm tubes.

THE LOWER MIDLITTORAL

The west shore

Owing to the irregular drainage of the sand flats on the west shore, some areas are a little drier than others. A transect (Fig. 5b) was taken through such an area situated below the *Phyllochaetopterus* zone and between two bands of *Diplanthera*. The dominant animal in the *Dotilla* association was *D. fenestrata*, of which the density, judging from burrows opening at the surface, was about 50/m². This population is less dense than in other places on the Inhaca shores. At low tide the juveniles remain feeding in the dry area during the whole of the period it is exposed, whereas the adults migrate following the tide downwards as it ebbs, and returning to their home sandbank with the flowing tide. They remain buried in the sand while the tide is high, and emerge again when it ebbs. Only if disturbed will they dig themselves in, with a corkscrew motion, while they are on wet sand away from 'home'. The burrows go down some 10 to 15 cm to the level of the reduced layers of black sand; such burrows are semi-permanent only, and collapse when covered by the tide. Unlike *Macrophthalmus grandidieri* from the wetter areas, *Dotilla* spends many hours a day in the air out of water. It occurs on sand at mid-tide level and on sand banks apparently much nearer to low-tide level, provided these are raised sufficiently above low-water level to ensure an adequate exposure to the air for feeding.

Animals found on the surface in these *Dotilla* areas include the following, which normally live among sand from this level downwards: the hermit crabs, *Clibanarius longitarsus* (de Haan), and *Diogenes avarus* Heller, the box crabs, *Calappa hepatica* (L.), and *Matuta lunaris* (Forsk.), a small round crab, *Philyra platychira* de Haan, and *Nassa arcularia* L. a scavenging snail.

The infauna is much less varied and not so abundant as in muddy sand. It consists mainly of scattered tubicolous worms. Locally common are the terebellids *Streblosoma persica* and *Loimia medusa*. The errant worm *Diopatra neapolitana* D.Ch. constructs tubes of a leathery material to which it adds pieces of gravel or shells, presumably collected while foraging. This worm may also be found on dryish sand further down the shore. The fusiform tubes of *Owenia* occur in small numbers all over the area. *Mesochaetopterus minutus* builds very narrow fragile sand tubes each about 10 cm long, massed together in clumps of several hundreds, forming little hillocks. Such hillocks may also be seen lower down the shore. *Gravierella multiannulata* Fauvel, *Clymene lumbricoides* Quatref., *C. natalensis* Day and *Magelona cincta* Ehl. are present. *Phyllochaetopterus*, the dominant worm of the previous zone appears to be completely absent.

Errant worms are not so common, a few specimens of *Nephtys tulearensis* and of *Pareulepis geayi* (Fauv.) and several species of *Glycera* have been found. The isopod, *Synidotea variegata* Coll. has also been seen in this area.

In the appearance of the surface the *Macrophthalmus grandidieri* association is very similar to the *Phyllochaetopterus* zone, but there is a spectacular decrease in numbers of this worm, which appears, therefore to congregate only around mean tidal level. The surface is somewhat more irregular owing to the presence of colonies of *Mesochaetopterus minutus* and *Diopatra neapolitana*, the tubes of both of which encourage the deposition of sand around themselves. The crab, *Macrophthalmus grandidieri*, while occurring sporadically in the *Phyllochaetopterus* zone is clearly dominant here. Unlike *Dotilla*, *Macrophthalmus grandidieri* is completely aquatic. Its burrows lead diagonally under the surface and are always almost full of water. The crab appears on the surface only when there is shallow standing water over the area, and remains in its burrow when the tide is very low and the surface of the sand dry. This crab feeds by licking sand grains and does not make pseudofaecal pellets, but it is also a scavenging and even a predatory animal. It does not stray far from its burrow and always rushes back when disturbed.

The most conspicuous members of the epifauna are the gastropods, *Polynices mamilla* L., several species of *Natica*, the commonest being *N. marochiensis* Gm., scavenging dog whelks, *Nassa arcularia* L. and *N. coronata* Brug., and the dingy *Melongena paradisiaca* (Mar.). Sometimes their shells are inhabited by hermit crabs, *Clibanarius longitarsus*, *C. padavensis* de Man. and *C. virescens* (Kr.) may be common especially near stones. *Diogenes avarus* Heller and *D. senex* Heller also occur, the latter being more common.

The commonest polychaetes of this association are *Ceratonereis erythraeënsis*, *Glycera subaena*, *Magelona cincta*, *Marphysa simplex* Crossl., *Nerine cirratulus* D.Ch. and species of *Scoloplos*, even though not more than three of each have been found in a square metre. The following polychaetes have in smaller numbers been found here:

Arabella mutans (Chamb.)
Armandia leptocirrus Gr.
A. longicaudata (Caullery)
Audouinia filigera D.Ch.
A. punctata (Gr.)
A. tentaculata (Mont.)

Ceratonereis costae (Gr.)
Cirratulus africanus Grav.
C. cirratus Mull.
Clymene lumbricoides Quatref.
C. natalensis Day
Dasybranchus caducus Gr.

Dasychone nigromaculata (Baird)
Glyceria alba Rathke
G. convoluta Kef.
G. prashadi Fauv.
G. unicornis Sav.
Goniada emerita A. & M.-Edw.
Gravierella multiannulata Fauv.
Hyboscolex longiseta Schm.
Leocrates claparedi (Costa)
Loimia medusa Sav.
Lumbrinereis papillifera Fauv.
Lysilla ubianensis Caul.
Nephtys tulearensis Fauv.
Notomastus aberrans Day
Orbinia foetida (Clap.)
O. monroi Day
Paralepidonotus indicus (Potts)

Parculepis geayi (Fauv.)
Parheteromastus tenuis Monro
Pectinaria papillosa Caul.
Phyllochaetopterus socialis Clap.
Pilargis falcata Day
Pista brevibranchia Cant.
Polyophthalmus pictus (Duj.)
Potamilla reniformis (O. F. Müll.)
Puliella armata Fauv.
Scolecopsis indica Fauv.
Scoloplos johnstonei Day
S. madagascariensis Fauv.
S. marsupialis South
Spiochaetopterus typicus Sars
Streblosoma persica Fauv.
Terebellides stroemi Sars

Bivalves appear to be extraordinarily scarce when compared with a temperate north Atlantic shore. Live specimens of *Loripes clausus* Phil., a white mussel, are only to be found occasionally although its dead shells are an important constituent of the substratum, forming dense masses with little silt between them over large areas. The brachiopod, *Lingula* sp. is quite common, its stalk buried deeply so that the shells open just at the surface. The burrowing brittle star, *Amphiopus integer* (Ljungman) is omnipresent, one or two at a time only, and two others, less common, have been found. *Amphiura delagoa* Bal. and *A. kalki* Bal., the latter usually in association with *Mesochaetopterus minutus*. A sea cucumber, *Holothuria hilla* Les. may be found in muddy sand at this level, though it is more usual under stones. *H. pervicax* Sel. is also present.

Isolated specimens of a white burrowing Cerianthid anemone may be found and several small enteropneusts including *Saccoglossus inhacensis* Kapelus and small specimens of *Balanoglossus hydrocephalus* v.d. Horst and of *B. studiosorum* v.d. Horst. Colonies of ascidians abound on the bare sand; they are tough and leathery in texture, some sand-encrusted such as *Polyclinum* sp., others more mucilaginous such as *Tridemnum natalense* Michaelson.

On the west shore the marine angiosperm, *Diplanthera uninervis*, grows rather sparsely but it is the outward mark of a rich infauna which may be called the *Diplanthera* association. One may still find, here and there, the burrows of *Macrophthalmus grandidieri*, but its sibling *M. bosci* Aud. is more numerous, especially if there are stones or boulders for shelter. As an associate of *Diplanthera* another marine angiosperm, *Halophila ovalis* (R.Br.) Hook.f. is common. This plant occurs in two forms, one with oval leaves and one with linear leaves; the former is more abundant and intermediates are quite easily found.

Many of the holes in the sand have been seen to be constructed by the pistol shrimp *Alpheus rapax* Fabr., which lives in pairs in slanting burrows reaching the water table a few centimetres below. Living commensally in the same burrow is a little goby belonging to one of several species of which *Cryptocentrus octofasciatus* Regan and *Gobius delagoae* Brnrd. appear to be the commonest. The holes are recognizable at low tide by the shell debris around the entrance and the grooves worked by the 'shrimps' in the entrance to the burrow.

A spectacular inhabitant of these flats is a white giant nemertean, over 1 m long and some 20 mm wide, with arrow-shaped head and long tubular cylindrical proboscis. It proceeds swiftly through the sand, writhing with sinuous motion, although there is no

pathway! Smaller greyish nemerteans also occur commonly as well as the pink *Baseodiscus hemprichi*. In this zone a giant enteropneust, *Balanoglossus studiosorum* v.d.Horst, the habits of which have been described by van der Horst (1940) is the most conspicuous species. Its large casts, up to 10 cm high and 8-10 mm in diameter, made of spirally coiled mucus-cemented sand, are scattered here and there about 5/m² among the plants. At the return of the tide the cast is destroyed to leave a mound of sand which is not colonized by *Diplanthera*. Other mounds of uncolonized sand are probably made by species of *Squilla*.

Just beneath the surface of the sand, sometimes making a little heap of black mud, and sometimes with a cast rather like a string of rabbit droppings, the grey cucumber, *Holothuria scabra* Jaeg. is half-buried. There are sometimes as many as 5/m².

The gastropods of the bare zone are less numerous among the *Diplanthera*, and another species of *Nassa*, *N. fenestrata* Mar. is commoner. It is frequently completely clothed in a felt-like covering of the hydroid *Podocoryne nassa* Millard. The little ringed cowrie, *Cypraea annulus* L. and sometimes the money cowrie, *C. moneta*, are abundant. In shallow pools there occur large numbers of *Haminea petersi* v. Martens and of *Atya cylindrica*. These may extend up at neap tide periods even to the *Phyllochaetopterus* zone. Crustaceans are numerous among these meadows. While the area is submerged Portunid crabs swim around; such are *Lupa pelagica* (L.) and occasionally *L. sanguinolenta* (Herbst), *Thalamita crenata* (Latr.), *T. prymna* (Herbst) and *T. admete* (Herbst). All disappear into holes either at this or a lower level as the tide recedes. The swimming spider crab, *Hymenosoma orbiculare* Desm. so common in *Zostera* fields further south, is abundant, but it is much smaller in size than specimens from the southern coast of the Union of South Africa. *Philyra platychira* de Haan and the box crabs, *Calappa hepatica* (L.) and *Matuta lunaris* (Forsk.) may be found but they prefer clean sand. The hermit crab *Pagurus fabimanus* M.-Edw. almost always in a *Tonna* shell is present. Several shrimps and prawns are common and may be found by digging just under the surface by day or by netting among the 'weed' as the tide ebbs at night. *Hippolyte kraussiana* (Stimps.), *Latreutes pygmaeus* Nob., *Pontophilus pilosus* Kemp, *Athanas minikoënsis* Cout., with *Penaeopsis hilarulus* de Man and *Penaeus canaliculatus* Olivier are the commonest while others such as *Processa aequimana* (Pauls.), and *P. japonica* (de Haan) and occasionally *Ogyrides striaticauda* Kemp have been found.

The polychaetes listed for the bare flats are also to be found here. Bivalves are constantly present but not in large numbers, and no one kind may be said to be dominant. The following have been recorded:

<i>Anadara natalensis</i> (Kr.)	<i>Maetra capensis</i> Sow.
<i>Cardium rubicundum</i> Rve.	<i>M. aequisulcata</i> Sow.
<i>C. rugosum</i> Lam.	<i>M. glabrata</i> Gm.
<i>Chione ambigua</i> Desh.	<i>Modiolus philippinarum</i> Hanley
<i>Circe pectinata</i> (L.)	<i>Psammobia bipartita</i> Phil.
<i>C. scripta</i> Lam.	<i>Siliqua polita</i> Wood
<i>Codakia punctata</i> (L.)	<i>Solen gouldi</i> Conrad
<i>Cutellus pellucidus</i> Pen.	<i>S. roseomaculata</i> Pilsbry
<i>Dosinia hepatica</i> Lam.	<i>Solenomya togata</i> Poli
<i>D. pubescens</i> Phil.	<i>Standella nicobarica</i> Gm.
<i>Glycymeris queckettii</i> Sow.	<i>Tellina madagascariensis</i> Gm.
<i>Loripes clausus</i> Phil.	<i>Tivela natalensis</i> Dunker

Occasionally green or buff burrowing Cerianthid anemones are found, in whose mucoid tubes colonies of *Phoronis ? australis* with jet-black lophophores are embedded. Juvenile specimens of *Modiolus philippinarum*, of *Pteria zebra* and of other pearl oysters

have been found in summer, attached to the leaves and stems of the plants of *Diplanthera*. *Dentalium octangulatum* Donovan and *Tonna galea* L. have occasionally been dug up.

The Saco da Inhaca and northern bay

The *Dotilla* association tends to begin at a higher intertidal level in these bays than it does on the west coast, but its lower level does not appear to have been similarly shifted upwards. When the tide covers the upper *Dotilla* patches, and in fact all *Dotilla* patches in the Saco and in the northern bay, flocks of greater flamingo, *Phoenicopterus ruber*, wander over them about knee deep stirring up the muddy sand with typical circling motion and would appear to feed on the small crabs they disturb. Certainly, they have been seen at low tide to wander along such banks and pick up and eat specimens from the surface. With *Dotilla* in these sandy patches are numerous specimens of *Loripes clausus*, at a density of around ten per square of side 25 cm, and a few specimens of *Dosinia hepatica* Lam. and *Tivela natalensis* occur with them. *Dosinia* was closer to the surface than *Loripes*. Occasionally *Psammodia bipartita* Phil. has been found. Polychaetes are common, including *Glycera subaena*, *G. convoluta* Kef., *Loimia medusa* and a striking nereid with alternating red and yellow bands, *Dendronereides zululandica* Day.

Over most of the area bordered above by mangroves the sand contains a very large number of empty shells of *Loripes clausus* and of *Dosinia hepatica* with occasional shells of other species. Sometimes these shells are so thick on the ground as to exclude *Dotilla* completely. Over a large proportion of the northern bay, but a smaller portion of the Saco *Dotilla* is most abundant on banks of pure sand of medium to coarse grain size.

In the lower portions of the shell debris there are a number of worms *Streblosoma persica*, *Owenia fusiformis*, *Armandia longicaudata* (Caull.), *Parheteromastus tenuis* Monro and species of *Scoloplos*, the sipunculid *Siphonosoma cumanaensis* and synaptid cucumber *Chiridota* sp. Accompanying the sipunculids in their burrows are tiny bivalves, *Montacuta* sp. and a yellow polychaete *Pilargis falcata* Day. No living representatives of the shells which constitute the most conspicuous feature of these shelly banks have been found amongst them.

A surprisingly large population of *Uca annulipes*, usually much paler in colour than those to be found among the mangroves, and of *U. marionis* occur on these banks. The former is in the more sandy areas and the latter burrow along the edges of the banks, and there is a considerable overlap. These shell banks must be very stable for over most of the area the surface layer of shells are overgrown by barnacles, *Balanus amphitrite* Darwin var *denticulata* Brock. In a few places close to the upper margin there are large aggregations of *Cerithium morus* Lam., a species common among rocks at a comparable level on the west shore.

As on the west shore the areas occupied by the *Macrophthalmus grandidieri* associations are covered with a thin superficial layer of water for most of the intertidal period. On the occasions when the water table leaves the surface it is never far below. This is apparently a necessity, for the burrows of *M. grandidieri* are always shallow. The slant of the burrows distinguishes them from the more vertical burrows of *Alpheus malabaricus* Fabr. which are also very common.

In front of the mangroves at the head of the Saco the crab and shrimp occupy a broad belt, the substratum of which is very muddy and into which one may sink, ankle deep. The density of crabs is high, about 30/m². In the mud they are accompanied by *Dendronereis arborifera* Peters, which is common, by glycerids, by species of *Scoloplos* and

by *Aonides oxycephala* (Sars), *Leiochone tenuis* Day, *Nerine cirratulus* (D.Cl.), *Nicomache mossambica* Day and *Polydora normalis* Day which are occasional; the last group are all long thin forms.

On the surface there are large numbers of the small carnivorous snail, *Nassa kraussiana* Dunk. a species highly characteristic of muddy estuaries in Southern Africa, but here it is not, as further south, accompanied by a commensal species of *Hydractinia*. Numerous juveniles of *Melongena paradisaica* Martini come to the surface through the silt when the tide rises. Small areas of mixed *Diplanthera uninervis* and of *Thalassia hemprichii* occur in this area but the fauna associated with the plants is the same as that in their immediate vicinity.

Along the western shore of the Saco *Macrophthalmus grandidieri* occurs in waterlogged fine sand. On the surface, here are numerous snails and hermit crabs of the same species as occurred on the west shore of the island. The infauna, mainly of polychaete worms is also similar to that of the west shore. The brittle star *Amphioplus integer* is not uncommon, while *Ophionephthys africana* Bal. and *Ophiophragmus sacensis* Bal. are present. *Saccoglossus inhacensis* occurs in drainage pools. In pools throughout this zone may be found large numbers of *Haminea natalensis* Kr. and *H. petersi* and of *Atys cylindrica*. These are preyed on by *Aglaja coerulea* v. Mart., a species of variable colour sometimes uniformly dark purple with blue edges to the parapodia and sometimes with a definite pattern of brown and orange patches but with the same blue-edged parapodia. That there are variants of one species is indicated by the finding of copulating pairs one partner of each colour strain. Occasionally *Chelidonura velutina* (Q. & G.) may also be found with them, and probably it too feeds on the abundant specimens of *Haminea* and *Atys*. The water in these pools may reach 36° C, quite uncomfortable to touch, but the tectibranchs are still very actively engaged in copulation and egg-laying.

Over almost the entire area of both bays where the *Diplanthera* association is present, *D. uninervis* is accompanied by *Thalassia hemprichii* as a co-dominant. The zone is named after the former because the latter is not confined to this intertidal level but extends downward into the infralittoral fringe. *Thalassia* is present in two distinct life forms. One is broad leaved and one is narrow leaved, and they seem to be randomly spread within the area of distribution. In the Saco this association covers large tracts of the intertidal flats, particularly on the eastern shore. On the western shore of the Saco only the upper portions of this association are well developed for the profile of the shore is not an even shape but nearly level in the upper midlittoral and in the lower levels it slopes very steeply, thus the lower portions of the *Diplanthera*-*Thalassia* flats are excluded. In the northern bay it is well developed throughout the whole extent of the bay. For the most part the fauna is similar to that of the west coast but in the warmer coves towards Ponta Torres and in certain backwaters towards Cabo Inhaca a richer fauna of more tropical species is found. This will be separately discussed (p. 109).

Towards the entrance to the northern bay, directly between the Portinho da Inhaca and the Ilha dos Portugueses, the facies shown by this association is very similar to that on the western shore of the island of Inhaca. In this area *Thalassia* is more sparse than elsewhere in the northern bay.

The more easterly portions of the northern bay and the eastern shores of the middle reaches of the Saco show a facies which includes a greater number of warm water species. At a first glance the surface of the warmer flats is seen to contain very many more bare mounds of sand. These may be the result of the activity of several animals. Firstly, some are the result of the faecal casts of *Balanoglossus hydrocephalus* and *B.*

studiosorum, but there is also another much larger form with a faecal rope some 25 mm in diameter; this species has recently been collected but not yet identified. Secondly, some are formed by cucumbers, *Holothuria arenicola* Jaeg. and *H. povicax* Sel., species which burrow downwards almost vertically, the anus alone remaining close to the surface. These cucumbers may reach a length of over 50 cm. Such mounds may readily be recognized by the presence of characteristic holothurian faeces at the summit, and stimulation will result in a jet of water from the anus of the cucumber. Thirdly, some of these bare mounds have a central depression with remnants of the faeces of some creature with a narrow gut. Associated with such mounds there is at a distance of around a metre or slightly less a depression, in the centre of which is a large round neatly mud-lined hole going more or less vertically downwards. Occasionally specimens of a species of *Squilla* have been seen at the entrance of such holes, but they are difficult to catch. The burrows descend some 75 cm and enter a series of tunnels branching underground. Once a large specimen of *S. nepa* Latr. was caught at the entrance to such a burrow in the Saco, and *S. woodmasoni* Kemp has been collected in similar situations in the northern bay. Hence it is probable that species of *Squilla* are responsible for mounds of this third type. Over the years the following squillids have been collected on the Inhaca flats by Professor C. J. van der Horst and his pupils but only rarely was any record kept of the sort of hole from whence they came: *S. hieroglyphica* Kemp, *S. latreillei* (Eyd. & Soul.), *S. nepa* and *S. woodmasoni*. Smaller species with similar habits which have been collected are: *Lysiosquilla acanthocarpus* Miers, *L. maculata* (Fabr.), *Pseudosquilla ciliata* (Fabr.), and *Odontodactylus scyllarus* L.

Among the plant cover are burrows of two distinct types. There are the burrows of an alpheid-goby commensal menage, as on the west shore, but the species concerned have not been identified. Such a burrow may be recognized by the lines leading from the entrance, up which the alpheid has been pushing sand when cleaning out the burrow. The second type is made by crabs of the genera *Thalamita*, *Charybdis* and *Lupa*, these are typically outlined by a number of sand-free empty shells of the types commonly found in the substratum.

The penaeid prawns, *Metapenaeus monoceros* (Fabr.), *Penaeopsis hilarulus* de Man, *Penaeus canaliculatus* Olivier, *P. indicus* M.-Edw., *P. monodon* Fabr. and *P. semiscalcatus* de Haan have frequently been dug out of the mud near the mangrove channels and at night may be caught as they swim freely around. Characteristically found in shallow pools and hollows at the lower levels of these *Diplanthera-Thalassia* flats are numerous sea-urchins: *Astropyga radiata* (Leske), *Diadema setosa* (Leske) juveniles only, **Echinometra mathaei* Blainv. *Echinothrix calamaris* (Pall.) juveniles only, **Salmacis bicolor* Ag., **Temnopleurus toreumaticus* Leske, **Tripneustes gratilla* (L.). Of these species those marked with an asterisk are always covered to some extent by fragments of shells, or with fronds from the sea grasses, a reaction which Millott (1955) has shown to be characteristic of tropical sea urchins.

Lying amongst the weeds are numerous black holothurians including *Holothuria edulis* Les. with reddish under surface, *H. impatiens* Forsk. which readily emits its Cuvierian organs, and *H. atra* with body coated by adherent sand grains.

Occasionally the two large starfish, *Pentaceraster mammillatus* (Aud.) and *Proto-reaster lincki* (Blainv.) may extend up this zone though they are more characteristic of the zone next below. Again the holothurians characteristic of the lower zones extend upwards into the lower regions of this *Diplanthera-Thalassia* zone.

Of the molluscs to be found on the surface the most conspicuous is usually *Cypraea*

annulus, and in some seasons species of *Strombus* chiefly *S. gibberulus* L. and *S. mauritanus* Lam. are very abundant. Predatory forms include several species of *Nassa* and of *Natica*, and *Polynices mamilla* is widespread. Species usually present in small numbers but which may on occasion be common include:

Prosobranchs:

Conus arenatus Hwass in Brug.
C. ceylanensis Hwass in Brug.
C. geographus L.
C. ebraeus L.
C. flavidus Lam.
C. lividus Hwass in Brug.
C. miles L.
C. natalis Sow.
C. textile L.
Cypraea annulus L.
C. arabica L.
C. carneola L.
C. caurica L.
C. chinensis L.
C. erosa L.
C. lamarcki Gray
C. moneta L.
C. tigris L.
Melongena paradisaica (Martini)
Monilia obscurus Wood
Nassa arcularia L.
N. coronata Brug.
N. fenestrata Marratt
N. kraussiana Dunk.
Natica didyma Bolten
N. imperforata Gray
Nerita albicilla L.
Polynices mamilla L.
P. (Naticina) sebae (Sonleyer)

Opisthobranchs:

Amplustrum amplustre (L.)
Dolabella gigas Rang
D. scapula (Martyn)
Glossodoris spp.
Gymnodoris ceylonica (Kel.)
G. citrina Bergh
G. inornata (Bergh)
Hydatina physis L.
H. velum Gm.
Melibe vexillifera (Bergh)
Pleurobranchus peroni Cuv.
P. perrieri Vayss.
Pleurobranchus sp. nov.
Pleurobranchaea sp.
Solidula solidula Lam.
Stylocheilus longicaudus (G. & G.)
Umbraculum sinicum (Gm.)

Bivalves:

Atrina aequilatera Martens
A. squamifera Sow.
Cardium rugosum Lam.
Chione ambigua Desh.
Circe pectinata (L.)
C. scripta Lam.
Modiolus philippinarum Hanl.
Pinctada capensis Sow.

On areas colonized by *Diplanthera* and to a lesser extent on *Macrophthalmus* areas there may occur patches of *Udotea orientalis* A. and E. S. Gaupp, the plants being scattered more or less evenly about 20/m² within each patch. Isolated clumps of *Acanthophora muscoides* (L.) Bory and *Caulerpa cupressoides* (Vahl.) C.Ag. are also common. Seasonally, particularly in summer, masses of the blue-green alga, *Lyngbya majuscula* Harv. form a felt smothering everything attached to the surface of the substratum.

The warmer coves and backwaters of the Saco da Inhaca and of the northern bay

In warmer coves towards the mouth of the Saco da Inhaca, behind Ponta Torres (Fig. 4), and in backwaters of the northern bay just below the lighthouse on Cabo Inhaca (see Fig. 3) a more tropical fauna is to be found. These coves and backwaters are sheltered from the strong east winds, and at times of low tide the temperature of the water remaining on the surface of the flats becomes high (35-37° C). The areas so warmed up are quite large, several hundred metres long and equally wide. In these areas the fronds of *Diplanthera* and of *Thalassia* are much longer and more luxuriant than in other areas on the island. Such fronds may reach up to 20 cm. Lying on the surface are clumps of various algae, sometimes loose and sometimes attached. The most conspicuous of these are *Boodlea composita* (Harv.) Brand, *Struvea anastomosans* (Harv.) Picc. &

Grün. ex Piccone, *Valonia aegagropila* C.Ag., *Chaetomorpha crassa* (Ag.) Kütz., *Turbinaria ornata* J.Ag. and *Gelidiopsis rigida* (Vahl.) Weber van Bosse. Clumps of corallines, *Amphiroa* sp. and *Jania* sp. are also common. All these algae appear to be more frequent in summer.

A most conspicuous feature of these warmer coves is the abundance of ophiuroids, *Ophiocoma scolopendrina* (Lam.) and *O. valenciae* (H. & T.) of which the former is much the more abundant. These brittle stars seek shelter in anything available. They may be

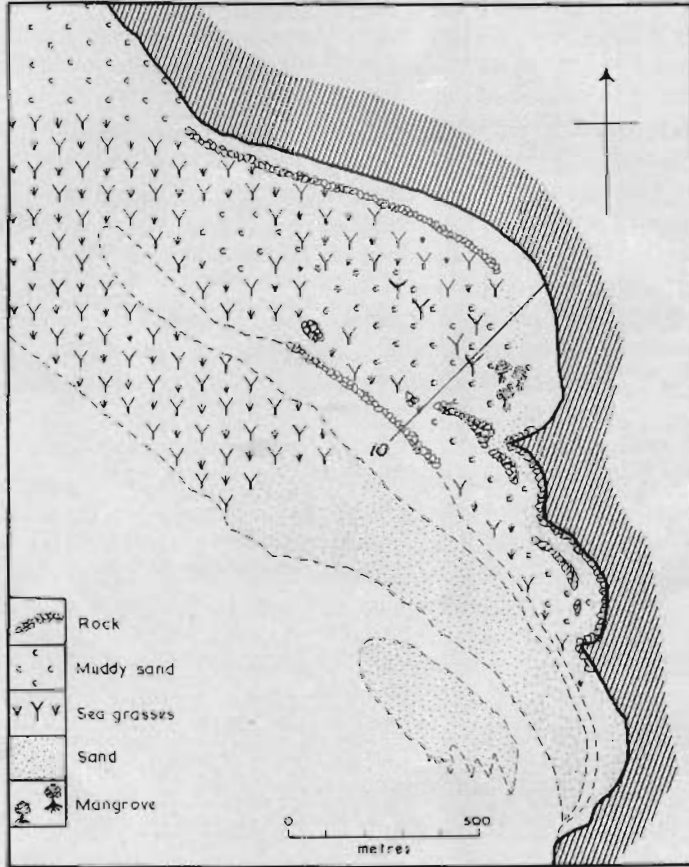


FIG. 4. A warm cove behind Ponta Torres. The rocky margin of the channel supports a coral reef. The numbered line indicates the location of the transect shown in Fig. 5f.

found in shells lying on the surface or half buried, under small stones, under clumps of algae, or even under the fronds of the 'sea grasses'. At low tide they are not visible, but when the tide reaches them on the flow the animals appear to wake up and two or three of their arms emerge to wave in the water seeking food. In specially favourable places they may reach a density of over 100/m². Individual specimens are then so placed that the tips of their arms only just overlap.

In some of the deeper pools on these flats there are large numbers of sea urchins, all those listed on p. 108 are present and in addition *Toxopneustes pileolus* (Lam.) Long

specimens of *Synapta oceanica* (Less.) and shorter specimens of *Ophiodesoma mauritiae* Hed. are stranded on the surface.

A hand net swept through the weed while the tide is flowing catches isopods, *Paranthura punctata* Stimps., *Lanocira latifrons* Stebb., *Paraciliacea mossambicus* Brnrd.; amphipods, *Cymadusa australis* (Brnrd.), *Erichthonius brasiliensis* (Dana); shrimps, *Pontophilus pilosus* Kemp, and species of *Periclimenes*.

Clumps of algae on the surface shelter two species of tanaid, *Leptochelia tenuis* (Thomps.) and another at present unnamed.

In addition to the species listed above (p. 109) the following are also conspicuous among the epifauna.

Porifera:

a greenish sponge not yet identified

Coelenterata:

Calliactis polypus (Forsk.) both commensal with hermits and apart from them.

Stoichactis sp.

a cerianthid with commensal *Phoronis* ? *australis*.

Polycladida

Several unidentified species

Crustacea:

Anchistus custos (Forsk.) commensal with *Atrina* spp.

Aniculus aniculus Fabr.

A. strigatus (Herbst)

Calcinus elegans M. Edw.

C. laevimanus (Randall)

Charybdis annulata (Fabr.)

C. cruciata (Herbst)

C. merguensis (de Man)

C. natator (Herbst)

C. orientalis Dana

Matuta banksi Leach

Monomia gladiator (Fabr.)

Pagurus asper de Haan

P. deformis M. Edw.

P. megistos (Herbst) with commensal anemone *Calliactis* sp.

P. setifer M. Edw.

Periclimenes brevicarpalis (Schenk.) commensal with an anemone *Stoichactis* sp.

P. rex Kemp commensal with *Hexabranchnus* and with *Synapta oceanica*

Pinnotheres doffeini Lenz commensal with *Atrina* spp.

Thalamita danae (Stimpson)

T. integra Dana

T. sima M. Edw.

T. wood-masoni Alcock

Troglopagurus jousseaumi Bouvier

Ophiuroidea:

Amphioplus squamata (D.Ch.)

Ophiactis modesta Brock

Ophiomastus venosa Peters

Placaphiothrix foveolata (Marktanner)

Opisthobranchia:

Ceratosoma cornigerum Ad. & Rvc.

Dendrodoris gemmacea (A. & H.)

Euselenops luniceps (Cuv.)

Hexabranchnus marginatus Q. & G.

Phyllidia ? *coelestis* Bergh

Large numbers of *Atrina squamifera* Sow. and of *A. aequilatera* Mart. are embedded in the substratum with the edges of the shells level with the surface of the soil. In places they are almost continuous but arranged in no special order. As elsewhere in the Saco and northern bays there are large mounds bare of plant cover and these are produced by a series of animals similar to those already described.

Characteristic of the substratum of these warm coves is a very large population of enteropneusts. The most abundant is *Ptychodera flava* Eschsch. which appears to be ubiquitous, and to be present in very large numbers, twenty have been taken from a square of side 14 cm. Where a high population of this enteropneust is present the surface of the soil presents a curious appearance of crumbs of sand held together by mucus spread all over the surface. *Ptychodera* also occur in clumps of algae on the surface, a strange site for a burrowing species. Other less abundant forms include species of *Balanoglossus* as yet undetermined, of *Glossobalanus alatus* v.d. Horst and of *Willeya delagoënsis* v.d. Horst. It would appear that in these areas the enteropneusts have taken over the role and the niche occupied by species of polychaete worms in more temperate shores.

In the areas populated by *Ptychodera* there are many specimens of *Pyramidella mitralis* A.Ad. Knowing that the Pyramidellidae is a family containing many parasites, one wonders if this species is parasitic on the enteropneusts. At low tide the animals are apparently resting and have not been found feeding.

Polychaetes are present with the enteropneusts, in smaller numbers, perhaps, than elsewhere on the island, but with a similarly wide range of species. Peculiar species include the aphroditids, *Harmothoë lunulata* D. Ch., and *Lepidasthenia* sp.; *Glycera rouscii* and a specimen 30 cm long of a *Dasybranchus* sp. was collected. In a nook of this bay, at the foot of a small cliff of beach sandstone, there has accumulated a bank of coarse sand colonized by *Calianassa kraussi*.

THE INFRALITTORAL FRINGE

At Inhaca the infralittoral fringe may be divided into two distinct plant zones, or plants may be entirely absent. Typically this fringe is under water at all except the very lowest tides. The organisms to be found here are such as are completely aquatic and cannot withstand drying.

The west shore

On the west shore the two plant zones are well developed. The uppermost is dominated by *Cymodocea serrulata* and *C. rotundata* the former being somewhat the more abundant. There is some admixture of *Thalassia hemprichii* and also of the two forms of *Halophila ovalis*, but though these two species are widespread they never become even sub-dominant. Towards the lower limits the cylindrically leaved *Syringodium isoetifolium* becomes a co-dominant. Slight depressions in the area in which the water lies more deeply are colonized by *Cymodocea ciliata* which is the characteristic plant of the lowermost part of the infralittoral fringe, extending downward into the channels. On the west shore *Thalassia* does not extend upwards into the zone dominated by *Diplanthera*.

Throughout the area occupied by *Cymodocea serrulata* the water on the surface is always around ankle deep or slightly less. The shrimp-goby associations, described above and *Balanoglossus studiosorum* are more evident at this level, and the holes made by swimming crabs are more numerous. Here echinoderms are commoner than at any other intertidal level. Sea urchins, *Tripneustes gratilla* and *Salmacis bicolor* with red and white spines, are both common. The former always, and the latter usually cover themselves with leaves of *Cymodocea* or other available debris when the tide is out. The pencil urchin, *Prionocidaris baculosa* (Lam.) and the dull-coloured *Temnopleurus toreumaticus* occur sporadically but are frequently abundant in the zone below. *Holothuria scabra* is common and *H. atra* (Jaeg.) is abundant. *H. atra* usually occurs at the surface but may be half-buried. Also on the surface but sometimes buried in the sand with the tentacles alone protruding are several sea cucumbers: *Actinopyga plebeja* (Sel.), *Holothuria arenicola* Semper, *H. cumulus* Clark, *H. leucospilota* (Brandt), *H. pervicax* Selenka, *H. impatiens* (Forsk.) and *H. parva* Lamp. The brilliant red *Protoreaster lincki* and the green or yellow *Pentaceraster mammillatus* may be frequent. The tropical brittle stars common in the warmer coves of the Saco and of the northern bay have not been found on the west coast.

Polychaetes are not so abundant as on the middle shore but most of the species listed above are present. In addition *Ceratonereis mirabilis* Kbg., *Etione ornata* Gr., *Platynereis dumerili* (A. & M-E.) and *P. isolata* Grav. occur. A fairly common feature is

the large U-shaped burrow of *Chaetopterus variopedatus* (Ren.) recognized by the ivory-lined openings about 20 cm apart. In this area too, very long wide leathery tubes penetrate over 30 cm into the sand. Some are inhabited by edwardsiid anemones and others by the aphroditid worm *Polyodontes melanotus* (Gr.).

As in the *Diplanthera* areas bivalves are on the whole scarce in number of individuals but various in species. The species listed above (p. 109) have all been found and again there are localized beds of the large pen shells, *Atrina squamifera* and *A. aequilatera*.

The base of the *Cymodocea serrulata* zone merges inconspicuously with the *C. ciliata* association. This zone is always covered with standing water, usually more than ankle deep. In the upper parts of its range *C. ciliata* tends to occur in more or less circular patches, and as one proceeds downwards these patches become confluent.

The epifauna of the previous zone is still present, and in places it may be rather more abundant. Because the area is constantly under water many fish are present. Four species of sea horses, *Hippocampus hystrix* Kaup, *H. novae-hollandae* Steind., *H. kuda* Blkr., *H. camelopardalis* Bianc., and the razor fish, *Aeoliscus punctulatus* (Bianc.) poise themselves among the weed; the flute mouth, *Solenostoma cyanopterus* Blkr. resembles a dead leaf of *Cymodocea* and is very difficult to see. Amongst the fish that are frequently netted are the following:

<i>Acanthopagrus berda</i> (Forsk.)	<i>Holocentrus diadema</i> Lac.
<i>Aeoliscus punctulatus</i> (Bianc.)	<i>H. sammara</i> (Forsk.)
<i>Amblyapistus binotata</i> (Peters)	<i>Hippocampus camelopardalis</i> Bianc.
<i>Amphiprion polyminius</i> (L.) (commensal with <i>Stoichactis</i>)	<i>Hyporhamphus delagoae</i> (Brnd.)
<i>Apodocreeidia vanderhorsti</i> de Beauf.	<i>Lactoria cornutus</i> (L.)
<i>Apogon novemfasciatus</i> (Cuv.)	<i>Naso brevirostris</i> (Val.)
<i>Apogonichthyooides uninotatus</i> (Smith & Rad.)	<i>Novaculichthys macrolepidotus</i> (Bloch)
<i>Atherina afra</i> (Peters)	<i>Pegasus draconis</i> L.
<i>Callyodon guttatus</i> (Schneider)	<i>Pelates quadrilineatus</i> (Bloch)
<i>Canthigaster margaritatus</i> (Ruppel)	<i>Pomacentrus annulatus</i> Peters
<i>Cheilio inermis</i> (Forsk.)	<i>Plotosus anguillararis</i> (Bloch)
<i>Crenidens crenidens</i> (Forsk.)	<i>Pseudopeneus pleurospilos</i> (Bleeker)
<i>Cryptocentrus octofasciatus</i> Regan (commensal with Alpheid)	<i>P. pleurotaenia</i> (Playfair)
<i>Cynoglossus lida</i> (Bleek.)	<i>Pseudorhombus arsius</i> (Hamilton)
<i>Dascyllus trimaculatus</i> (Rupp.) (commensal with <i>Stoichactis</i>)	<i>Scorpaena mossambica</i> Peters
<i>Duymaeria flagellifera</i> (Val.)	<i>Scorpaenodes guamensis</i> (Q. & G.)
<i>Echidna nebulosa</i> (Ahl.)	<i>Secutor insidiator</i> (Bloch)
<i>Gobius delagoae</i> Brnd. (commensal with Alpheid)	<i>Siganus oramin</i> (Schneider.)
<i>G. spence</i> Smith	<i>S. rivulatus</i> (Forsk.)
<i>G. stagon</i> Smith	<i>Sillago sihama</i> (Forsk.)
	<i>Syngnathoides biaculeatus</i> (Bleeker)
	<i>Synodus variegatus</i> (Lac.)
	<i>Therapon theraps</i> Cuv.

Spider crabs which, apart from the tiny *Hymenosoma orbiculare*, have not been encountered higher up the shore are abundant at this level. The largest of them is *Parthenope horrida* (L.) which may frequently be found crouching among the weeds near rocks. *Menaethius monoceros* (Latr.), is often of the same brilliant green as a new leaf of *Cymodocea* to which it clings. Another, *Micippe thalia* (Herbst) with bent rostrum has the carapace overgrown with a coralline alga, *Jania* sp. which is also an epiphyte on the stems of *Cymodocea ciliata*. More frequent in summer is *Cyphocarcinus capreolus* (Pauls.), an almost cylindrical crab which has fixed a stolon of *C. ciliata* to the rostrum. Until the present records this crab had not been found south of the Red Sea. *Schizophrys aspera* M.-Edw. is also common. Occasionally the long-legged *Macropodia formosa* Rathbun, and *Platylambrus quemvis* Steb. and the rare little calthrop crab, *Eunedomus*

granulosus McGilch. have been found. Sponge crabs, *Dromia dormia* (L.), *Dromidia unidentata* (Rüpp.) *Cryptodromia pentagonalis* Hilg. and *Pseudodromia rotunda* (McLeay), are occasional and may carry on their backs colonies either of sponges or of zoanthids or of the ascidian *Polyclinum* sp. This ascidian is common on bare or sparsely covered flats at this level.

The only brittle star at all common among *Cymodocea ciliata* is the tiny *Ophiothela beauforti* (Engel). But others such as *Amphiura kalki* Bal., *Ophiactis carnea* (Ljung.), *O. savignyi* (M. & T.) and *Placophiothrix proteus* (Koehl.) have occasionally been found.

The commonest gastropod *Cantharides fultoni* (Sow.) appears to feed on the plants. Large cowries, such as *Cypraea arabica*, *C. talpa*, *C. tigris* are occasional. The surface is frequently strewn with specimens of *Malleus anatinus* Bosc.

The plants are overgrown by several sessile and colonial forms; *Botryllus planus* Van Name is present on a large proportion of them; the alcyonacean, *Cespitularia caerulea* is frequent; hydroids are abundant, and while *Lytocarpus philippinus* (Kirch.) is the most conspicuous the following also occur:

Amphisbeta minima (Thomps.)

Campanularia integra MacGill

Clytia johnstoni (Alder)

Dynamena quadridentata (Ellis & Sol.) var. *nodosa*
Hargitt

Obelia spp.

Pennaria disticha Godfuss var. *australis*

Sertularella spp.

Sertularia linealis Warren

Thyroscyphus fruticosus (Esper.)

A zoanthid, *Palythoa natalensis* grows on sand between the plants, as do the alcyonaceans, *Spongioderma chuni* Kük., *Telestes arborea* Wright and Stander. Attached to the stems of the plants are other alcyonaceans, *Anthelia flava* (May), *Heteroxenia elizabethae* Köel., *H. fuscescens* (Ehrb.) and *H. rigida* (May).

Conspicuous among the patches of *Cymodocea ciliata* because they stand up like a branching twig 20 cm high above its level are colonies of a Eunicid worm, *Eunice tubifex* Cross. These worms secrete a tough, leathery tube, attached to some buried stone, piece of coral debris or shell. The tube is U-shaped, the base being downwards and the two ends free; these free ends may have one or several openings, each at the end of a short branch.

The bare sandbank — Astropecten association

The bare sandbank which interrupts the *Cymodocea* associations at the edges of the channel is quite narrow in the region chosen for transect purposes; it is non-existent in several places, for example at the entrance to the Portinho da Inhaca. In the neighbourhood of Ponta Rasa it is very strongly developed, and it is also extensive in certain areas of the northern bay behind the bar between Cabo Inhaca and the Ilha dos Portugueses. The sandbanks extend upwards to a higher intertidal level than do the adjoining *Cymodocea* meadows and normally are exposed at low water of spring tides. The fauna of these low level sandbanks is identical with the fauna of sandy areas which are not exposed but which at low water remain covered ankle-deep with water. Hence they are considered to present a facies of the infralittoral fringe. The fauna occurring here and forming the *Astropecten* association is quite different from that among the *Cymodocea*. The sand is such that permanent burrows cannot be made in it, there is no reduced layer and the sand is much better oxygenated than over the remainder of the flats.

The animal most abundant on these flats is *Astropecten granulatus*, which lies buried just under the surface of the sand. There may be as many as 5/m². It feeds exclusively on the myriads of tiny *Assimineae* sp. that litter the surface of the sand, swallowing them

whole and passing the shells after the contents have been digested. Rarely another species *Alubina fulva* (Watson) has been found in stomach contents. Another starfish *Astropecten acanthifera* feeds in the same way on larger molluscs such as the topshell *Cantharides fultoni*, *Mitra rufescens* A. Ad. and other species of *Mitra*, and bivalves in the sand such as *Circe pectinata*. The purple sand dollars, *Echinodiscus auritus* Leske and *E. bisperforatus* Leske may be traced by the outline of the shell in the sand, as they lie just beneath the surface. The former is commoner than the latter. Almost every specimen carries on the lower surface a pair of tiny brittle stars, *Amphylicus androphorus* Mott. the female of which is larger than the male.

Occasionally a very large brittle star, *Ophiocentrus dilatatus* (Koehler), with arms some 20 cm long and coloured brilliant orange with interrupted mauve bands round the arms, has been found. The tiny disc lies fully 20 cm below the surface while the arms are visible above. The almost cosmopolitan heart urchin, *Echinocardium cordatum* (Penn.) is quite common, and *Holothuria pervicax* occasional, both buried in the sand. Associated with the sand dollars is the curious crab, *Dorippe dorsipes* (L.) which carries a specimen of *Echinodiscus*, living or dead, on its back, held in position by the last two pairs of legs which are dorsal in position. The crabs which are characteristic of this sandbank are those which can bury themselves easily by sidling into the sand and which do not have permanent burrows, included are:

Box crabs:

Calappa hepatica (L.)
C. gallus (Herbst)
C. lophos (Herbst)
Matuta lunaris (Forsk.)
M. banksi Leach

Round crabs:

Myra fugax (Fabr.)

Philyra platychira de Haan

Sand crab:

Ranina ranina (L.)

Masked crab:

Gameza bicornis Gray

Hermits:

Clibanarius padavensis de Man

In some areas there are communities of pennatulids, chiefly one with a tall orange stem and purple polyps, *Virgularia gustaviana* (Herklots). Another is a purple clavate form with small paler polyps, *Cavernularia lütkeni* Köll. Others present are *Actinoptilum molle* Kük., *Veretillum cyanomorium* Pall., and *V. leloupi* Tixier-Durivault.

Ploughing just beneath the surface are numerous specimens of *Philine aperta* (L.) and carnivorous moon shells, *Natica taeniata* Menke, and the large white slimy *Sigaretus planulatus* Recluz, with foot up to 10 cm long and shell hidden beneath the propodium and epipodium. Other carnivorous gastropods include:

Conus geographus L.
C. lividus Hwass in Brug.
Fasciolaria trapezium (L.)
Mitra rufescens A.Ad.

Murex ramosus L.
Ranella crumena Lam.
Thais mancinella L.

The most conspicuous gastropods are terebrids; the small buff *Terebra monilis* (Q. & G.) is most common during some years, the large fawn *T. dimidiata* or the orange *T. straminea* Gray at other times; pyramidellids, chiefly *Obeliscus dolobratu*s L. may be so frequent that there are 5-7/m². These are always found base upwards and the terebrids are apex upwards. Several bivalves have been found but none are really common, they include: *Tellina madagascariensis* Gm., *T. vulsell*a, *Cultellus pellucidus* Pen. *Solenomya occidentalis* Koch. Along the edge of the sandbank, on the slopes of the channel there are the tubes of a brown cerianthid anemone. Abundant is *Sipunculus indicus* Peters living in deep vertical burrows. Small specimens of amphioxus, *Branchiostoma lanceolatum* (Pallas) *B. helcheri* (Gray) and *Asymmetron lucayanum* Andrews have also been found on these

banks. The only enteropneusts found in the clean sand is *Balanoglossus studiosorum*. Very few polychaetes occur, mainly malidanids such as *Gravierella multiannulata*, and *Clymene lumbricoides* and most abundantly *Nephtys tulearensis*.

The Saco da Inhaca and the northern bay

Over much of the Saco there is no community dominated by *Cymodocea serrulata* and in fact both this species and *C. rotundata* are uncommon throughout the bay. Chiefly this is due to the profile of the shore. The shore slopes gently and gradually through the *Diplanthera* zone and then at the edge of the channel becomes steep, so that over large stretches the portion of shore which one would have expected to be occupied by the *Cymodocea serrulata* association is pinched out of existence.

In the middle reaches of the Saco *Syringodium isoetifolium* is found in the lower levels of the *Diplanthera-Thalassia* association and so one might presume that these plants have come down to a lower intertidal level. The presence of many echinoderms, both asteroid and echinoid among the lower levels of the *Diplanthera* zone is also suggestive of this. Only towards Ponta Torres, in the warmer coves is there a distinct *Cymodocea serrulata* zone and it is quite narrow and interrupted by the rocky platform on which the coral reef has developed. The fauna associated with it is similar to that of the adjacent lower levels of the *Diplanthera* zone except that the thalassinid *Axius* sp. with vertical burrows is conspicuous in the sandy gravel available to it. Wherever it occurs the *Cymodocea ciliata* zone is in all respects similar to that on the west shore.

All three facies represented on the western shore in the infralittoral fringe are to be found in the northern bay. Towards the mouth of the bay between the Portinho da Inhaca and the Ilha dos Portugueses the zonation is exactly as has been described for the west shore except that there is no bare sand bank and that there are more individuals of the various species recorded. For some undetermined reason this whole area seems to be able to support a more abundant population of both animals and plants.

The fields of *C. ciliata* are particularly luxuriant. Individual stems are less than 10 cm apart and the ground is completely covered with vegetation. The plants flower abundantly and freely. The stems of the plants are densely colonized by coralline algae, such as *Corallina cubensis* Mont., *C. cuvieri* Lamour. and other unidentified species. The stems and leaves are colonized by hydroids, as listed above p. (114). Colonies of the ascidians, *Botryllus planus* and more rarely *Eudistoma rhodopyge* (Sluiter) are to be found on the junction of leaves and stem and extending on to the leaves. Several species of pearl oyster most commonly *Pinctada natalensis* and *Pteria zebra* cling by byssus hairs to the stems and the hammer-shaped *Malleus anatinus* litter the ground in small groups.

On the surface of the sand under cover of the plants are several lumps of coral, chiefly *Pocillopora damicornis bulbosa* Ehrb. and *P. verrucosa* Ellis & Sol. with the solitary Fungid *Herpetolitha limax* Esper. occasional as well as other *Fungia* spp. Several species of Alcyonaceans, some massive, and some slender are also quite common. Large pelagic anemones have occasionally been found. The swimming crabs mentioned above dart among the plants and their holes are abundant. Spider crabs are frequent as on the west shore.

Clusters of the scallops *Chlamys tinctus* Rve. *C. layardi* Desh. (= *nicobarica*) and *C. coralnoides* D'Orb. (= *noduliferus* Sow.) and of the pearl oyster *Meleagrina margaritifera* are frequent. These are very much more abundant here than elsewhere on the island. Aggregations of *Atrina aequilatera* and *A. squamifera* are common and a third species

A. bicolor Gm. is frequent. This species does not bury itself so that the edges of the shells are level with the surface of the ground as the other do, but it is only partially buried, at least half of the shell is upstanding. Additional burrowing species of bivalves are *Tellina immaculata* (Phil) and *T. rostellum* Hanley, *Lioconcha hebraea* (Sow.) *Codakia exasperata* Rve. and gastropods *Tonna variegata* and *Mitra arenosa* Lam.

All the echinoderms recorded from the west shore are here but in greater numbers, and in addition the cidarid, *Eucidaris metularia* frequently with commensal *Ophiothela beauforti* Engel coiled round one or more spines. *Prionocidaris baculosa* is abundant and frequently attached to the larger spines are several specimens of *Capulus intortus*.

In addition to the animals listed on p. 109 the following molluscs have been collected: *Fasciolaria trapezium* L., *Hexabranhus marginatus* Q. & G., *Peristernia leucothea* Mel., *Urosalpinx heptagonalis* Rve., and *Arca navicularis* Lam.

Further into the bay it would appear that, as in the Saco, the *Diplanthera* zone, here also with a luxuriant growth of *Thalassia* as co-dominant particularly in the lower levels, extends downwards to occupy the upper margin of the infra-littoral fringe, thus the *Cymodocea serrulata* zone is reduced in width but it does not disappear. The animals occurring with it are those which are to be found on the west shore, and a large proportion of those which occur in the *Diplanthera-Thalassia* zone extend downwards. The *Cymodocea ciliata* zone shows the same facies as elsewhere.

On the extensive sandbanks there have been found the same series of animals as on the western shore.

ANIMAL PARTNERSHIPS AND COMMENSALISM

Partnerships between animals on the shores of Inhaca are common, as indeed they are on mud and sand flats in many parts of the world. Mention has been made of the partnership between a 'shrimp', and gobies in the lower midlittoral and infralittoral fringe. Pairs of *Alpheus rapax* and of *A. rapacida* construct burrows, and gobies, *Cryptocentrus octofasciatus*, *Gobius delagoae* and others take up residence. The gobies perch on their pelvic fins at the entrance to the burrow, as though on guard; meanwhile the shrimps scoop out the sand and shells that clog the burrow, pushing the debris before them with the big chela as they move slowly up from below. They return backwards. Any slight disturbance causes gobies and shrimps to disappear into the burrow until they consider it safe to resume. Such an association of alpheid shrimps and gobies is common, it is mentioned by Bayer & Harry-Rofen whose photograph (1959, Pl. 14, Fig. 1) might well have been taken at Inhaca. A similar association between *Alpheus crassimanus* and *Gobius nudiceps* has been recorded by Macnae (1957) from the Zwartkops mudflats near Port Elizabeth. Although *Alpheus crassimanus* has been found at Inhaca no commensal gobies have been seen with it. On the soft mud of the Saco da Inhaca one finds burrows of *A. malabaricus* and small skipping gobies, *Butis butis* Hamilton occur with it.

The large sea anemone, *Stoichactis* sp. is almost always accompanied by small fishes, *Amphiprion bicinctus* Rüppell and *Dascyllus trimaculatus* (Rüppell). This partnership is well known and the association of other species of these genera has recently been studied by Davenport & Norris (1959). Less well known is the association of the prawn, *Periclimenes brevicarpalis* with the anemone. This prawn, translucent with opaque whitish, orange and purplish areas has not, at Inhaca, been found apart from the anemone. The basis of this relationship has not been studied. An occasional specimen of *Saron marmoratus* has been found crawling over the anemone but since this prawn is

more commonly found under stones and coral debris its presence on the anemone is considered to be fortuitous.

A second species of *Periclimenes*, *P. rex*, has been found, on one occasion, a royal blue, associating with *Synapta oceanica*, and on several occasions a brilliant scarlet, accompanying the large nudibranch, *Hexabranchnus marginatus*, the colour of which it exactly resembles. Again the slate-pencil urchin, *Eucidaris metularia*, is frequently accompanied by the calthrop crab, *Eumedomus granulatus*.

Less spectacular partnerships involve several of the echinoderms on the flats. *Echinometra matthaei* affords shelter between its spines to a small alpheid prawn, *Arete indica* Coutière. The colour of this prawn closely resembles that of the urchin which may be grey, purplish or reddish, and they are most difficult to spot as they crouch among the spines. At most one pair, a male and a female have been found on one urchin, rarely only one; but seldom has an unaccompanied urchin been picked up.

The starfish *Linckia multifora* and the black holothurian *Holothuria atra* are almost invariably accompanied by aphroditid polychaetes. *Linckia multifora* shelters in its ambulacral grooves an undescribed species of *Harmothoe*. *Gastrolepidia clavigera* Schmarda crawls over the body of *Holothuria atra* in colour exactly resembling its host. The worm leaves rapidly whenever the host is picked up.

Other commensal aphroditids have been recorded, *Hololepidella nigropunctata* (Potts) lives on the ophiuroid *Macrophiothrix hirsuta* (Müll & Trosch.). *Harmothoe lunulata* and *Lepidasthenia* sp. (cf. *michaelseni*) are associated with large enteropneusts and sipunculids in their burrows. Another polychaete, *Pilargis falcata* also accompanies these enteropneusts and sipunculids and *Harmothoe lunulata* has been found associating with *Ptychodera flava*.

These sipunculid burrows also shelter the tiny bivalve mollusc *Montacuta* sp. which lives either attached by a byssus thread to the worm or attached to the wall of the burrow itself.

The tough leathery tubes of *Chaetopterus* and of *Eunice tubifex* give shelter to various small crabs and aphroditid worms. Each *Chaetopterus* tube houses a pair of procellanid crabs *Polyonyx biunguiculatus* (Dana). The upright branching tubes of *Eunice* shelter several commensals, a crab, *Chlorodopsis areolata* M.-Edw.; the aphroditid worms, *Leonnates decipiens* Fauv., a species of *Harmothoe* and one of *Lepidonotus*; the terebellid *Thelepus triserialis* and two brittle stars, species of *Ophiactis*.

Commensalism between echinoderms is illustrated by the presence on almost every specimen of *Echinodiscus* of either species, of several specimens of a small whitish ophiuroid, *Amphylicus androphorus* Mort., the males of this species are tiny and sit on the oral side of the larger female.

Almost every specimen of *Atrina*, no matter what the species shelters within the mantle cavity a pair of small alpheid prawns, *Anchistus custos* and females of the pea crab *Pinnotheres doffeini*. An unidentified species of *Pinnotheres* is also commonly found within the mantle cavity of *Modiolus philippinarum*.

The well-known symbiosis of hermit crabs with anemones is represented at Inhaca by the association of *Pagurus megistos* with *Calliactis polypus*. Only rarely have the two been found apart; the anemone more frequently than the hermit.

Dromiid crabs are frequent, *Dromia dormia* always carries a sponge; *Pseudodromia rotundata* carries a colony of the leathery ascidian *Polyclinum* sp.; *Cryptodromia tomentosa* carries a colony of *Trididemnum*; and *Dromidia unidentata* carries a colony of the zoanthid *Palythoa*.

In some respects certain parasitic associations would seem to be readily derivable from a one-time commensal partnership. We have mentioned the association of the capulid prosobranch, *Capulus ungaricus* with *Prionocidaris*. Another capulid, *Thyca ectoconcha* Sarasin, is present as a parasite on about one in thirty specimens of *Linckia multifora*. Larger specimens are invariably female with the dwarf male on her 'neck' and hidden beneath the limpet-like shell. The proboscis of the female penetrates deeply into the body wall of the host.

Also parasitic on *L. multifora*, but much less common than *Thyca* is *Stylifer linckiae* Sarasin, an eulimid prosobranch.

In certain areas *Holothuria scabra* is heavily parasitized by *Mucronalia* sp. Off the Portinho da Inhaca approximately one in twenty-five specimens of *Holothuria scabra* were infected, between Ponta Rasa and Ponta Punduini no infected specimens were found on 437 specimens examined during the same week as the other count was made.

H. scabra is frequently parasitized, too, by numerous specimens of a pyramidellid 5-10 mm long, *Odostomia* sp., which cling to any part of the body but more particularly to the membrane around the base of the tentacles and allow themselves to remain attached when the tentacles are withdrawn. Knowing the parasitic habit of this family of prosobranchs one wonders if *Pyramidella mitralis* which is found in colonies of *Ptychodera* is parasitizing the enteropneust. They have never been seen to do so, but they have never been found apart from the acorn worms.

SHIFTING OF COMMUNITIES

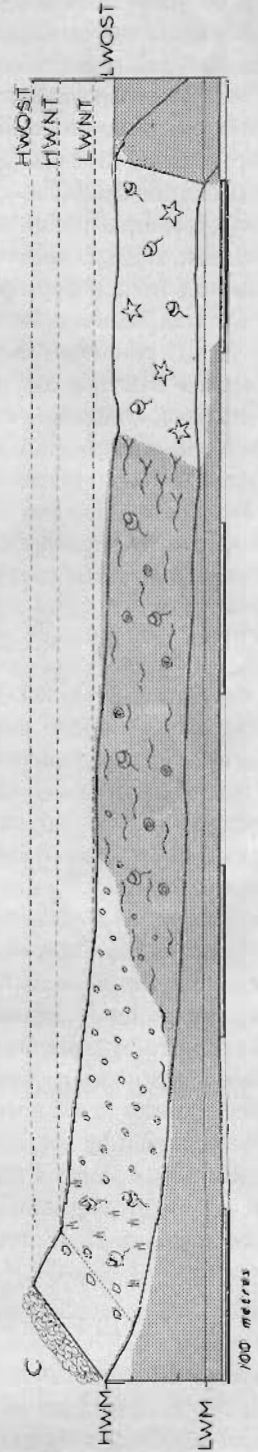
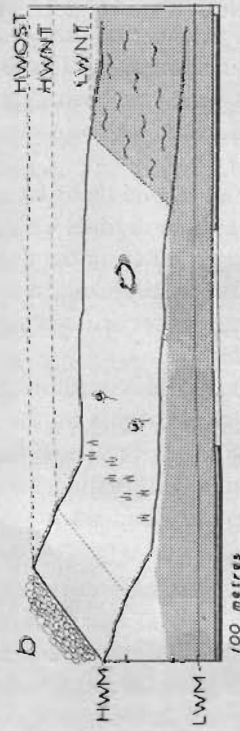
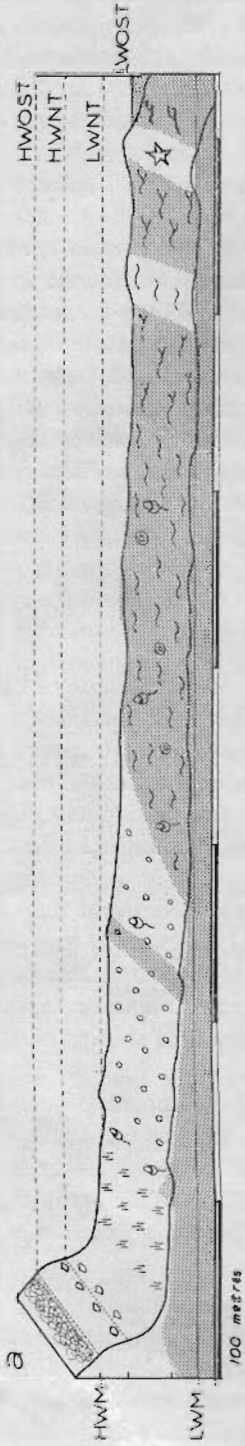
Over the years there have been slight variations in the extent and distribution of the plant and animal associations and communities. Occasionally at extreme low tides tracts of *Cymodocea* have been exposed to the heat of the sun and have died. Recovery by the same species has followed rapidly in some cases. In others the removal of the plant cover has altered the tidal currents and sand has been deposited, smothering any chance of recovery and so establishing a sandbank which in due course is colonized by an *Astropecten* association.

The *Dotilla*, *Macrophthalmus* and *Diplanthera* facies of the midlittoral may replace one another as conditions vary from time to time. Changes in tidal currents may dissipate the sand of a *Dotilla* area, flattening it, altering the distance of the water table below the surface, and so rendering it suitable for colonization by *Macrophthalmus* or *Diplanthera*. Areas occupied by these may become better drained as a result of the shifting of drainage channels and so become suitable for *Dotilla*.

At some places in the northern bay sand is accumulating on the upper levels, extending the area occupied by species of *Ocypode*. Again on the south shore of the island between Ponta Rasa and Ponta Punduini storms have torn away the beach at higher levels to expose the underlying sandstone, thus obliterating the population of *Donax* in the area. Such changes are slight and temporary and do not affect the main features of shore topography.

EFFECTS OF SHELTER AND WAVE ACTION

The shores of Inhaca illustrate certain effects of different degrees of shelter from wave action. The eastern shore of the island is fully exposed to oceanic waves, and as a result slopes steeply from a high level down to low water mark. The effective intertidal range is increased by the fetch of the waves so that the vertical height between high tide mark and



- | | | | | | |
|--|-------------|--|----------------------------|--|--------------------|
| | Halophytes | | Sesarma | | Dotilla |
| | Avisennia | | Uca | | Ocypode |
| | Cerriops | | Macrophthalmus grandidieri | | Donax |
| | Rhizophora | | Alpheus and goby | | Phyllochaetopterus |
| | Diplanthera | | Axius | | Astropecten |
| | Cymodocea | | Enteropneusts | | |



FIG. 5. *a*, the zonation on transect 5 across the west shore opposite the marine station; *b*, the zonation on transect 6 on the uppermost portion of the west shore some 400 m north of the marine station; *c*, from transect 7 across a sandbank behind Ponta Rasa; *d*, the zonation on transect 8 in the northern bay; *e*, from transect 9 on the shore of the Saco da Inhaca; *f*, the zonation on transect 10 across a warm cove behind Ponta Torres. Stippling indicates areas with water on the surface at low tide.

low water mark is greater than the amplitude of the tide would suggest. Also a direct result of the waves and the slope of the beach is the highly specialized fauna, poor in numbers and variety. Above and around H.W.M.O.S.T. are the burrows of the pink ghost crab, *Ocyropoda kuhli*; and around high water of neap tides are many *Donax incarnata* (Gm.); following the tide up and down between mean tidal level and low water swarms of *Bullia natalensis* Kr. and *B. rhodostoma* Rve. act as scavengers on any cast-up animal matter; also following the tide over the same range are specimens of the mole crab, *Emerita austro-africana* Schmitt, an animal difficult of capture.

The western shore has some slight wave action, the result of wind waves produced in the bay. Certain areas of the Saco da Inhaca and of the northern bay show the effects of almost complete shelter with no wave action apart from the rare occasions when the wind blows from some exceptional direction. At Inhaca there are no shores with the substratum unconsolidated to a considerable depth. Such shores have been studied by the authors at Ambatozavavy on Nosy bé, off northern Madagascar.

The transition from fully exposed ocean shores to partially exposed shores may be sudden. On one side of a point the beach is exposed, on the other sheltered. The transition from partially exposed shores to shores with very little wave action is gradual. Day (1959) has pointed out that 'increasing shelter reduces the vertical height of the intertidal zone ... until it corresponds with the tidal range', and further that on sandy beaches 'under sheltered conditions the intertidal zone is broad with extensive flat areas towards the low tide mark'. At Inhaca on all shores except the ocean shore, the vertical height of the intertidal areas is very close to the tidal range. The profiles of these shores indicate, further, that with increasing shelter the flat areas extend upwards closer and closer towards high water mark thus rendering available areas for colonization by mangroves and supralittoral fringe associations of animals and plants. In relation to this flattening of the shore there are variations in the distribution of animals. On the western shores of Inhaca the *Dotilla*, *Macrophthalmus* and *Diplanthera* associations occur at levels below low water of neap tides. In the Saco and in the northern bay these associations occur up to and occasionally above the level of high water of neaps. Thus on the west shore, these associations do not reach to their potential upper levels but are prevented from doing so by the marked change in slope just below the tidal mean. Such a change in slope reflects the strength of wave action.

In Fig. 5 are represented a series of perspective block diagrams of Inhaca shores. Figs. 5a and b were prepared from surveyed transects (nos. 5 and 6) across the west shores near the Biological Station. The others have been prepared from aerial photographs and confirmed locally. Two of the diagrams (Fig. 5d and e) illustrate shores where wave action is minimal. The others are of shores with some wave action, as a result of which there is a steep upper shore, but note that the steep slope begins at a lower level on the shores illustrated by Fig. 5a and b; these two have the greatest exposure to wave action.

The diagrams indicate that the community or association which predominates at any locality is that which develops at the level where the intertidal flats are most extensive. On the west coast the zones below the steep upper slope are of more or less similar width, and the slope from mean tidal level downwards to a depth below low water of springs is quite even. In the Saco (Fig. 5e) the *Dotilla-Macrophthalmus-Diplanthera* flats predominate, and the *Cymodocea* zones are pinched by the steepness of the channel banks, a result of strong tidal currents around low tide. In the northern bay there are two facies; alongside the channel entering from the west (Fig. 5d) the slope is gentle and the succession complete with all zones well developed; in the eastern half, parallel to the

peninsula ending in Cabo Inhaca, is a facies similar in many respects to that in the Saco with the upper midlittoral levels well developed. Fig. 5c passes through a lower midlittoral with *Astropecten* on a sandbank thrown up where opposing tidal currents meet. Fig. 5f passes across the small bay near the entrance to the Saco behind Ponta Torres described above, p. 109. This transect shows the succession in an area with a marked tropical stamp. To be noted is the presence of a coral reef on the edge of a channel and behind the reef a belt in which the dominant animal is *Axius* sp., a zone highly distinctive of the area of debris just shoreward of a coral reef in the tropical waters of northern Madagascar.

In addition to determining the extent of the spread of various communities, shelter and reduction of wave action sometimes affect the nature of the communities through variations in the degree of consolidation of the substratum. At the head of the Saco in a *Macrophthalmus* area of muddy sand into which one sinks calf deep and the values for silt and clay are higher than usual, the dominant crab is accompanied by *Alpheus malabaricus* instead of *A. rapacida* which occurs only on firmer ground. There is also a spionid worm fauna characteristic of these relatively unconsolidated areas (the species are listed on pp. 106-7). Areas of soft muddy sand within the mangrove swamps are colonized by *Upogebia africana*; and at the other extreme coarse sand in the lagoons near Ponta Torres are colonized by *Calianassa kraussi*.

It has been customary to express the character of the substratum in terms of particle size. To this end a preliminary analysis was undertaken on the west shore across the transect illustrated above (Fig. 5a), and in the Saco across 360 m from mean tide level towards the central channel, using samples at intervals of 33 m. The variable amounts of shell and other debris in the samples made comparisons meaningless. When figures were adjusted so that particles over 0.5 mm in diameter were neglected, only three categories of sand texture were found. First the sandy slope of the upper west shore consisted mostly of coarse (>0.36 mm) and medium (>0.2 mm) grains, the smaller particles having been washed out by wave action; it differed from the steep wave-beaten east shore which was composed mainly of very coarse (>0.5 mm) and coarse grains. Secondly the *Astropecten* sandbanks at lower levels were composed of fine sand (<0.2 mm). Thirdly areas occupied by the dominant organisms, *Phyllochaetopterus*, *Dotilla*, *Macrophthalmus*, *Diplanthera* or *Cymodocea* were intermediate in texture, mixtures of particles ranging from coarse (8-30%), medium (22-75%), and fine (10-46%); the ranges found in each zone overlapped those found in the others. It appeared therefore that a quest for a correlation between sand particle size and the animal and plant communities was fruitless. Measurements of silt and clay using a Bouyoucos hydrometer (Piper 1944) also yielded few differential factors. There was no silt nor clay in the *Donax* and *Astropecten* sands. In other areas on the west shore there was a low but more or less constant amount of silt, slightly higher in the *Phyllochaetopterus* areas and in the more sheltered Saco. More exact analyses of the type recommended by Morgans (1956) were therefore not undertaken.

In general it would appear that the distribution of organisms across the flats at Inhaca is controlled by the level of the water table rather than by variations in particle size. In a few cases, however, the distribution of certain organisms depends directly on the degree of consolidation as in the species of *Alpheus* just mentioned. Both the level of the water table and the degree of consolidation are the resultants of a complex of variable water movements including tides, varying in strength and speed at different tidal levels; currents other than tides; and drainage of the shores coupled with wave action and shelter from wind. The degree of consolidation and the texture are both capable of alteration by

biotic factors such as sifting by the feeding activities of *Dotilla*, binding by tubes of *Mesochaetopterus* and stolons of the 'sea grasses' and by the feeding activities in deep burrows of *Calianassa*. Accumulations of shell debris varying in size from entire shells to particles comparable to the particles of silt, alters the nature of the substratum considerably and may well be a major factor in producing the character of the substratum of the flats at Inhaca. Observations at Inhaca and elsewhere have indicated that these two factors, level of water table and degree of consolidation, are between them sufficient to make possible comparisons between communities on the flats at Inhaca and other tropical and temperate shores.

ZONATION

Although the extent of the development of communities on the flats varies on different shores of the island there is a common pattern of zonation, described on p. 97 and designated by the names of the dominant genera. An attempt was made in general terms by Dahl (1952) to align the zonation of organisms of sandy beaches with the system proposed for rocky shores by Stephenson & Stephenson (1949). Dahl showed that there was a subterrestrial or supralittoral fringe dominated by talitrid amphipods and ocypodid crabs, a midlittoral with cirrolanid isopods, and a sublittoral or infralittoral fringe of rich and varied fauna. He suggested that crabs of the genus *Ocypode* replaced talitrid amphipods on warmer shores. This requires modification. Talitrid amphipods require cast-up wrack or other vegetation for shelter and for food and are abundant wherever this occurs on tropical or on temperate shores. But cast-up wrack is rare on tropical shores; hence over large areas talitrid amphipods are scarce but it is doubted if they are entirely absent. At Inhaca they are present wherever torn off fronds of the 'sea grasses' are cast up. The needs of species of *Ocypode* appear to be less specialized; hence they appear to replace the amphipods when in reality they are only more conspicuous. At Inhaca cirrolanid isopods are present in the midlittoral but not conspicuous. Again other organisms are more readily observed, hence more useful in designating a zone or sub-zone. Observations at Inhaca are therefore in agreement with Dahl's scheme.

Macnae (1957) has compared zonation on South African estuarine mud and sand flats with similar areas elsewhere. The application of this comparison may now be extended to more tropical shores. At first sight few direct comparisons can be made. The supralittoral fringe with an Arthrocnemetum and talitrid amphipods is directly comparable. The mangrove in the upper littoral occurring between the base of the Arthrocnemetum and the level of high water of neaps has no parallel on the south coast of Africa. Similarly the Spartinetum of the south coast of Africa, which occurs between high and low water of neaps has no parallel on Inhaca shores. But such a zone is present on South American shores between the base of the mangrove and low water of neap tides (Gerlach 1958). The fields of 'sea grasses' cover the same area as does *Zostera* but do not penetrate to such an high level.

ZOOGEOGRAPHIC CONSIDERATIONS

In Table I will be found an analysis of the further distribution of the species of polychaete worms, decapod crustaceans, echinoderms, gastropods, both prosobranch and opisthobranch, and bivalves which have been found in the soft substrata at Inhaca. This analysis indicates that the Inhaca fauna has strong affinities with the tropical Indo-west-Pacific and less strong affinities with the cooler waters of the Union of South Africa. These

proportions are similar to those on the rocks of the west shore of Inhaca (Kalk 1958). An analysis of the total number of species (Kalk 1959) shows a greater tropical component in the fauna, the result of the inclusion of reef-building corals which, strictly speaking are not intertidal.

It is of interest that a considerable proportion of all species found at Inhaca occur also on Australian shores. One of these is of interest: *Pyura stolonifera* (Heller) is confined to rocky overhangs in the warmer waters of the Indian Ocean but further south, e.g. at Zwartkops near Port Elizabeth and at Knysna it occurs also on sand flats, rooted by long processes of the test; presumably the high temperature on the flats at Inhaca precludes their colonization.

The presence of large fields of *Diplanthera*, *Thalassia*, *Syringodium* and *Cymodocea* gives a tropical stamp to the flats at Inhaca. Only *C. ciliata* has been found to flower and set seed, and that only on the flats. It occurs also intertidally on the east coast rocks but never flowers there. Of these sea grasses only *C. ciliata* extends into Natal at Sordwana Bay in Zululand. The temperate water species *Zostera capensis* is abundant at Durban, at Richard's Bay and at St Lucia. At Kosi Bay midway between St Lucia and Inhaca, Broekhuysen & Taylor (1959) record sparse vegetation on the flats but do not identify it. It would appear, then, that Inhaca is the southern limit of these tropical plants.

Table 1. *The geographic composition of the fauna of sand flats at Inhaca island*

	Total	Indo-west Pacific	Cape	Ubiquitous
Polychaeta	82	54	4	24
Crustacea (Decapoda)	125	113	2	10
Echinodermata	43	37	—	6
Lamellibranchia	46	45	—	1
Gastropoda: Prosobranchia	18	17	—	1
* Opisthobranchia	41	24	8	2

* Seven opisthobranchs are new species described or to be described shortly from Inhaca and not as yet recorded elsewhere.

Comparing the dominant animal communities of Inhaca with those to the southward, one also finds differences. *Dotilla fenestrata* is reported by Day & Morgans (1956) as abundant in Durban Bay in a similar niche to that occupied at Inhaca. On the other hand *Macrophthalmus grandidieri* is less conspicuous and apparently does not dominate an association. The levels at which these two crabs occur are occupied by associations dominated by *Upogebia africana* if the bottom is of mud or muddy sand, or by *Calianassa kraussi* if sandy. These two burrowing prawns are the dominant animals in estuarine flats of the south coast of the continents (Day, Millard & Harrison 1952, Scott, Harrison & Macnae 1952, Macnae 1957). Both occur at Inhaca but in very circumscribed habitats: *Upogebia africana* being abundant in the mud on the banks of the mangrove channels and within the mangrove swamps; *Calianassa kraussi* in a bank of sand sheltered by a rocky outcrop in the bay behind the coral reef near Ponta Torres. There is also a change in intertidal level where *Upogebia africana* is concerned. On the south coast of the continent it occurs below low water of neaps. At Durban around low water of neaps and at Inhaca it has only been found above high water of neaps. It was found at a comparable high level at Nosy Bé, in northern Madagascar. Is this a shift up the shore with decreasing latitude similar to that described by Gislen (1943)? Perhaps! but also at Inhaca and at Nosy Bé it is only in mangrove swamps and their vicinity that sandy muds of consistency and composition similar to those on the flats at Zwartkops and Knysna are to be found.

The tropical element is most marked in the lower intertidal levels and in particular in two regions of the flats; towards the mouth of the Saco and along the eastern section of the northern bay; but why, particularly in these areas? It has been found that when temperatures were taken simultaneously on the flats of the west shore off the biological station and in the small bay behind the Ponta Torres coral reef, the latter were consistently higher than the former. These two warmer areas are sheltered from the prevailing south and east winds and so the water on the flats does not get cooled by the wind blowing over it. Pools and shallow water left on the flats at high levels and in the fields of *Diplanthera* and *Thalassia* reach temperatures of 37° C. At such temperatures many animals show signs of distress if stranded. Crabs of the genera *Thalamita* and *Lupa*, sea hares such as *Dolabella*, and octopuses have been found dying. On the other hand tectibranch molluscs, *Haminea* spp., *Aglaja coerulea* and the little purple spotted sea hare, *Stylocheilus longicaudus*, crawl around, actively feeding, copulating and laying eggs. At the other extreme of temperature, no animals have been seen suffering from low temperature distress. The inshore cold current does affect distribution on the rocky ocean shore (Kalk 1958) but presumably it does not penetrate into the bay.

Few comparable areas in other parts of the world have been studied. Well studied areas include the lagoons along the northern shores of the Gulf of Mexico, lagoons on the Brazilian coast, and several stretches of the shores of Queensland. Of these the Queensland shores are the more comparable. The shores of Moreton Bay near Brisbane have been described briefly by Stephenson (1957), and these appear to be more similar to the flats at Richard's Bay than to those at Inhaca. In both, species of *Zostera* are present and *Calianassa* dominates; *Dotilla* conspicuous at Richard's Bay is replaced by the closely related *Mictyris*. The region of the Low Isles has been subjected to two detailed studies, by Stephenson, Stephenson, Tandy & Spender (1931) and by Stephenson, Endean & Bennett (1958). The reef flats show some similarities to certain Inhaca beaches. Particularly the areas termed the 'sand flats' and the 'Thalamita or stony flats' have equivalents at Inhaca and these areas have several algae, sea grasses and animals in common.

More oceanic coral reefs studied by American workers in the Pelew islands (Bayer & Harry-Rofen 1957) and in the Tuamotus (Morrison 1954) differ in that even though the fauna of the reef flats remains similar, the flora differs in the apparent absence of 'sea grasses' except for a species of *Enhalus* at Pelew. This robust plant does not occur at Inhaca but is common at Nosy Bé.

The authors have recently had an opportunity to visit Nosy Bé. Here the aspects of many of the shores is strikingly similar to the warmer coves at Inhaca. Apart from a greater abundance of corals and alcyonaceans in the lagoons and among the 'sea grasses' few differences were noted. The dominant plants and animals were frequently the same and the majority of the decapod crustacea and the molluscs found at Nosy Bé have also been found at Inhaca. The remainder were Indo-west-Pacific forms which do not reach so far south as Inhaca. Similarly no significant differences in pattern were found in Northern Moçambique at lat. 15° S, although 25% of the common species found there did not occur at Inhaca (Kalk 1959). The affinities of Inhaca are, then, with tropical areas and it may be accepted that here at 26° S we find a tropical outpost. This tropical fauna is sustained by the proximity of the warm Moçambique current and by the fact that the waters in the Bay of Lourenço Marques and the adjoining shallow coastal waters are warmed by the sun during periods of low tide. The lowest tides occur around mid-day, the insolation is great so the waters are warmed to temperatures higher than the air above them.

There is some variation in numbers of many of the tropical species. In some years species of *Strombus* and *Terebra monilis* are very abundant in others rare. Similarly there are variations in the numbers of the pleurobranchid opisthobranchs and in the sea hare, *Stylocheilus*. In some years juvenile 'pearl oysters', *Pteria* and *Malleus*, are abundant; in others less noticeable. All these forms tend to be abundant in the same years, which suggests that in these years the Moçambique current contributes more water to the bay, and that at the same time the cool counter current from the south is less strong.

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SUMMARY

In this paper, the first study, so far as the authors are aware, of the distribution of animals and plants across tropical sand and mud flats exposed at low tide, will be found descriptions of the zonation of the animals and certain plants on the flats at Inhaca island near Lourenço Marques in Moçambique, East Africa. The flats exposed at low tide are extensive some being up to 4 km from high water mark to low water level.

Close on 400 species of animal have been recorded from these flats.

The following zones are recognized:

1. A supralittoral fringe of two facies (a) dominated by Ocypodid crabs and Talitrid amphipods on semi-exposed shores, (b) the landward edge of a mangrove swamp with *Sesarma* spp., *Uca* spp. and talitrid amphipods on sheltered shores.
2. An upper midlittoral of varying facies: on semi-exposed shores dominated by *Donax faba* on a sandy slope and a community of tubicolous polychaetes on the flat at the base of the slope; on sheltered shores this area is replaced by the lower levels of the mangrove swamps with various combinations between.
3. A lower midlittoral of three facies (a) a community on dry sandbanks dominated by *Dotilla fenestrata* (b) a community on waterlogged banks of muddy sand dominated by *Macrophthalmus grandidieri* and (c) on areas with water lying on the surface a community of which the most conspicuous organism is the 'sea grass' *Diplanthera uninervis*.
4. An infralittoral fringe dominated by (a) spp. of *Cymodocea* if the area is covered by standing water and (b) by *Astropecten* if the area is a sandbank.

Discussions follow on the effects of shelter and wave action, on the associations of animals with one another and on zoogeographical implications.

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ADDENDUM

On the eve of going to press we have been informed by Dr M. A. Pocock of Rhodes University, Grahamstown, that Dr J. E. Dandy of the British Museum (Natural History) has identified *Zostera capensis* Setchell from material collected in the warm cove behind Ponta Torres, which has been described in some detail on p. 109. It may well prove that *Zostera* is more widespread and that much of the fine-leaved 'sea grass' in more sheltered areas and at unusually high levels is in fact *Zostera*. *Diplanthera*, which in its vegetative phase closely resembles *Zostera*, will then be restricted to lower levels and to the less sheltered shores.