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Intertidal Zonation at Aldabra Atoll

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Intertidal zonation at Aldabra Atoll

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[Plate 15]

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Introduction

This paper describes the general features of the zonation of animals and plants on the intertidal predominantly rocky shores of Aldabra. Because of the great diversity of the fauna and flora in the shallow sublittoral, identifications and the collation of data are as yet incomplete. Consequently this account is limited to the true intertidal and the actual shoreline (parts of the seaward platform which project into the eulittoral are not included here). The major distribution of organisms on the shallow seaward platforms, in the channels and in the shallow lagoon, will be discussed in a further paper.

Field work was carried out from 15 August 1697 until 9 January 1968 thus enabling observations to be made in both seasons. Intertidal studies were made at many sites around the island representing a complete range of exposure conditions. Because of inaccessibility, much of the north shore of Middle Island and the southwest shore of South Island was not examined.

(*a*) Zonation studies

The zonation of organisms upon rocky intertidal surfaces is a phenomenon recognized on shores throughout the world (Stephenson & Stephenson 1949; Doty 1957; Southward 1958*a*; J. R. Lewis 1964). The inclusion of the less obvious zonation of organisms on soft substrate shores into the universal scheme developed for rocky shores is a fairly recent development (Baissac, Lubet & Michel 1963; Morton & Miller 1968).

Until recently there had been few studies on intertidal zonation in the tropical Indian Ocean and in tropical seas in general. The situation in the Indian Ocean has been partially rectified by recent studies on rocky and sandy shores in Mozambique (Kalk 1958; Kalk & Macnae 1962), Mauritius (Hodgkin & Michel 1963; Baissac *et al.* 1963); Madagascar (Pichon 1964; Plante 1964; Picard 1967); Mahé, Seychelles (Taylor 1968); Singapore (Purchon & Enoch 1954) and the Red Sea (Klausewitz 1967; Safreil & Lipkin 1964).

Studies on the intertidal in all these areas have been limited to the description of zonation patterns and the distribution of organisms upon the shore. Apart from tidal data and an assessment of exposure no attempt has been made to measure physico-chemical factors affecting shore organisms. Further there have been few studies in the tropics on the detailed biology of individual species such as that by Struhsaker (1966), which might lead to an understanding of the observed zonation patterns. This situation is likely to exist for some years to come.

Aldabra is an excellent site for the study of intertidal zonation because:

(1) There is an almost continuous land rim so that an uninterrupted comparison of zonation patterns around the atoll can be made.

(2) There is a strong contrast between conditions on exposed and sheltered sites.

(3) The limestone substrate is fairly uniform so that substrate effects on the distribution of organisms are minimal.

(4) A ready assessment of the long-term exposure factor at any one site may be given by the shape of the cliff profile.

(*b*) *The zonal terminology*

The zonal terminology used here is that of J. R. Lewis (1964) which was in turn derived from that of Stephenson & Stephenson (1949). The zonal scheme depends upon the fact that certain types of organisms characterize certain positions upon the shore. The zonal divisions on rocky shores are fairly sharp but those on soft substrates have boundaries which are less distinct. The three zones recognized and the organisms which characterize them around Aldabra are listed below.

1. *The littoral fringe*

This is characterized on rocky shores by the presence of *Littorina* and blackening organisms such as blue-green algae and lichen. The zone extends from, at the bottom level, the first appearance of abundant barnacles to the upper landward limit of *Littorina* at the top. On sandy shores the zone is characterized by the crab *Ocypode ceratopthalma* and on muddy shores with mangroves by the crab *Sesarma*.

2. *The eulittoral zone*

On rocky shores this zone is characterized by the occurrence of barnacles, limpets and the gastropod *Nerita*. The zone extends from the upper limit, the first appearance of abundant barnacles, to the lower limit at the first appearance of corals, marine phanerogams and the algae *Turbinaria* and *Sargassum*. The top of the barnacle zone is used as a major reference point in shore description throughout the world even though, as Ballantine (1961) has pointed out, no one is quite sure what the barnacle line means in terms of physical conditions. On sandy shores around Aldabra the fauna is so sparse that the limits of the zone are indistinct but it is characterized by the bivalve *Atactodea glabrata*. On muddy shores in mangroves the eulittoral zone extends from the first appearance of the fiddler crab *Uca* to the lower limit at the first appearance of *Thalamita*.

3. *The sublittoral zone*

This zone is characterized in shallow levels by corals, marine phanerogams and the algae *Turbinaria* and *Sargassum*. In places the shore levels uncovered by only the lowest spring tides have a distinctive fauna and flora and can usefully be divided off as the sublittoral fringe. On coral reefs and reef limestone shores the extensive development of wide platforms at the immediately sublittoral level exposes the organisms inhabiting them to a wide range of environmental variations. The organisms are subjected to occasional emersion, restricted water circulation, high insolation, wide temperature, oxygen and carbon dioxide variation and heavy rain. The reef-flat or sublittoral platform thus behaves as a sublittoral fringe pool of the constantly varying surface level type (Doty 1957).

2. Physical factors influencing zonation

As yet the physical factors affecting the distribution of animals and plants on the shores of Aldabra have received little attention and most parameters can only be assessed in qualitative terms.

(*a*) *Climate*

The climate of Aldabra is discussed by Farrow (this volume, p. 67). It appears that actual air conditions of temperature and humidity do not accord closely with those experienced at or immediately above the substrate surface (J. R. Lewis 1964). Heavy rain at low tide may exert considerable influence on intertidal populations. Seasonal changes in air temperature on Aldabra would not be expected to have any affect on intertidal organisms.

(*b*) *Wave action*

The assessment of wave action or exposure on any shore is still largely qualitative and depends very much on the experience of the observer, but in any area useful comparative assessments can be made. The degree of wave action is related to the direction and strength of the wind, configuration of the shore and the depth of the water offshore. The prevailing winds around Aldabra are the southeast Trades which blow strongly and consistently from April until October. Thus the shores of the south and east of the atoll will experience the most severe exposure conditions. The highest exposure is seen from around Cinq Cases to Point Hodoul. Shores on the north and west of the atoll experience less exposure; however, at times during the northwest monsoon high wave action occurs but it is neither so continuous nor severe as on the south and east shores. On the exposed shores salt spray is driven continuously inland for a period of several months. The presence of the seaward shallow sublittoral platform has an important effect upon wave action. At low water most of the wave action is transferred from the base of the cliffs to the seaward edge of the platform. Therefore organisms which could survive on a shore with continuous wave splash may be eliminated by this effective calm period at low spring tides. On lagoon shores the wave action experienced at any time is less intense than on the seaward shores. The northern shore of the lagoon which is exposed to wind-generated waves from the southeast Trades experiences more wave action than the southern shore which lies to the lee of South Island.

As shown by Stoddart *et al.* (this volume, p. 31) an assessment of the long-term exposure conditions acting upon a shore can be made by a study of the cliff profiles. Thus sheltered shores have low undercut cliffs, with increasing exposure the profile changes to vertical and then steeply inclined landwards. With more exposure the cliff becomes ramp-like, wider and at the most exposed sites a stepped profile is developed with the appearance of a midlittoral platform.

(*c*) *Tides*

The information at present available on the tidal régime for Aldabra is discussed by Farrow & Brander (this volume, p. 93).

The presence of the wide and level seaward platform on the seaward shores of the atoll means that for the low eulittoral and sublittoral fringe zones a fall of a few centimetres in tidal level will cause widespread emersion upon the platform.

The tidal drainage and fill of the almost landlocked lagoon takes place through the four channels which are of varying sizes. In consequence tidal lags of up to several hours are experienced in the lagoon. The tidal lag is variable from place to place and as yet the tidal régime within the lagoon is poorly understood. It appears that a body of water in the central lagoon merely moves back and forth with the tides and is never or infrequently renewed. Frequent renewal of water takes place only in the vicinity of channels at the west and in extreme east of the lagoon. The distributions of organisms in the shallow sublittoral of the lagoon and the channel areas are strongly affected by the complex drainage and circulation patterns.

(*d*) *Temperature, insolation and desiccation*

These three factors are inextricably interwoven and in the tropics would seem to be very important factors influencing the distribution of intertidal organisms.

The temperatures of sea water in open circulation around the seaward shores are unlikely to rise to a level approaching the lethal temperatures of intertidal animals. Rock pools on the south and east coast do experience extreme temperature changes. Lagoon water gives temperatures a few degrees higher than those of the open sea but the difference is not considered significant in terms of the distribution of intertidal animals.

Air temperatures particularly those caused by insolation have more effects on the distribution of organisms than sea-water temperatures (Doty 1957). Because of desiccation effects studies on the lethal temperatures of intertidal animals have been carried out on animals immersed in sea water (Broekhuysen 1940; Southward 1958*b*; Evans 1948). It has been established (Brown 1960; Broekhuysen 1940) that desiccation is an important factor controlling the distribution of animals upon the shore. More work is needed in the tropics on substrate temperatures, actual temperatures reached by the animal and the desiccation effects. Such work as has recently been done in California indicates that the temperatures reached within the mantle cavity of the limpet *Acmaea* may be up to 5 °C higher than the air temperature 3 cm above the substrate surface (Hardin 1968). Preliminary results of temperature recordings using *Nerita textilis* made on Aldabra in September 1969 show animal/air/substrate temperature differences of a similar order of magnitude.

(*e*) *Substrate, topography and aspect*

With one exception all the substrates available for colonization by intertidal organisms around Aldabra are calcareous. These may be limestone cliffs, beach-rock, cobbles, boulders, sand or (the non-calcareous exception) mangroves. On the limestone cliffs minor substrate differences may be seen, caused by differential solution in the low and high littoral; thus the tops of the cliffs are minutely dissected but the lower areas are relatively smooth. Beach-rock exposures are broad and dip shallowly seawards, the surface is relatively smooth but dissected by regular jointing, forming deep crevices. Minor facies variations in the limestone may form local differences in the porosity and water retention properties of the rock causing local variations in the distribution of organisms. Local variations in microtopography may be caused by the organisms themselves, e.g. calcareous algae and barnacles.

The area beneath the undercut on the cliffs of the north and west coasts and the lagoon are shaded for a good portion of the day being exposed to direct insolation only in the early morning and in the late afternoon. The rock surface beneath the overhang retains dampness for much of the low tide period and sites with dripping water are common. At sites with severe undercutting the lack of illumination is probably an important factor limiting the distribution of algae. On the south and eastern shores the cliffs are wide and ramp-like and are exposed to high insolation and the only shade present is that in gullies dissecting the cliffs, the undercut in the sublittoral fringe and the microtopography of the limestone.

The relatively soft limestone substrate is very suitable for exploitation by intertidal boring organisms such as barnacles, bivalves and echinoids.

(*f*) *Salinity*

In sea water covering the seaward shores of the atoll little variation in salinity would be expected from that of normal sea water. Reduced salinities would be expected in certain parts of the lagoon at times during the wet season. All shore-living animals must be able to withstand incursions of rain water to some extent and the combination of heavy rain in the wet season with low spring tides must affect shore populations. This will possibly affect plants and animals which have settled in the area during the dry season rather than the permanent populations.

3. Descriptions of zonation patterns

Zonation patterns at a series of selected sites around the atoll are described and illustrated below. Beginning with sheltered seaward shores, sites experiencing increasing exposure are discussed. These are followed by a description of zonation on the shores experiencing the special conditions in the lagoon and channel areas.

(*a*) *Sheltered shores*

On sheltered shores such as the western and northern shores the cliffs are about 3.5 m in height and undercut to a greater or lesser extent by an intertidal notch (figures 1, 2). This notch is about 2.5–3 m in amplitude above the e.l.w.s. level. Above the notch the cliff face is vertical for 1 to 2 m but at the summit is deeply and intricately dissected. The depth of the notch into the cliff is variable, usually 2 to 3 m it may be as much as 10 m in extreme cases. In any one length of cliff such as near Anse Var (0685, 12050) all gradations in depth of undercut may be seen. The cliff flattens out at about l.w.s. level to form a basal platform which descends gradually to the shallow sublittoral platform. A subsidiary shallow notch may be present between the basal platform and about 1.5 m above it. At spring tides the basal platform may be emersed at low water and the top of the main notch may be covered at high water. Along ome parts of the coast particularly along the northern shore of Middle Island at the foot of the cliff there is a trough-like depression parallel to the cliff, up to 1 m deeper than most of the seaward platform, which retains standing water at low spring tides.

(i) *Anse Var* (grid reference 06850, 12050)

High on the top of the cliff *Littorina glabrata* is found among crevices in the intricately dissected rock surface. On the vertical face above the cliff *Nerita plicata* is found in open positions. A little lower and extending into the undercut *N. undata* is common occupying more shaded sites than *N. plicata*. The crabs *Geograpsus stormi* and more commonly *Grapsus tenuicrustatus* are found at this level but at low water range all over the eulittoral.

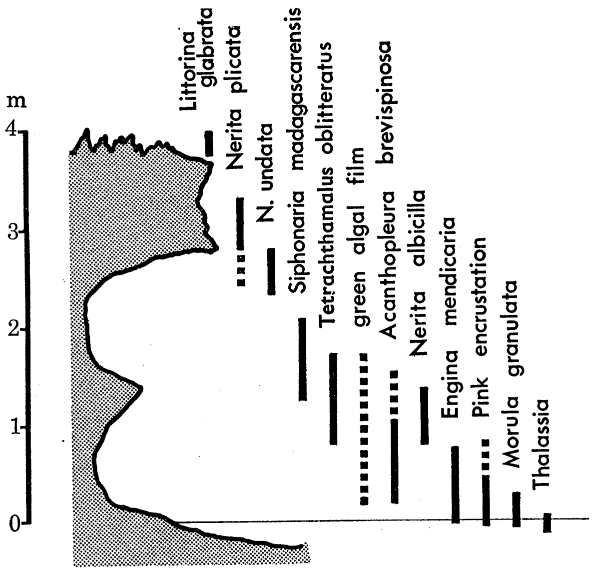

FIGURE 1. Zonation of intertidal organisms on cliff at Anse Var (06850, 12050).

At about 2 m above the basal platform the top of the eulittoral is marked by the presence of the barnacle *Tetrachthamalus oblitteratus* the limpet *Acmaea*, the pulmonate limpet *Siphonaria madagascarensis* and the large chiton *Acanthopleura brevispinosa*. A green film of blue-green algae is present over the rock surface. The cliff face is here shaded by the projecting overhang so that usual cryptofauna forms such as *Nerita albicilla* and a pink colonial ascidian occur on open surfaces. At other transects nearby a tubiculous eunicid worm occurs throughout most of the mid-eulittoral zone. The boring barnacle *Lithotrya* may also occur, the abandoned holes of which may be occupied by a small anemone. Mollusca typical of this level are the predatory *Engina mendicaria*, *Morula granulata*, the chiton *Acanthopleura* and in the lowest positions *Morula uva*.

On the basal platform at the foot of the cliff algae are more abundant and forms such as *Pocockiella*, *Dictyurus*, *Laurencia*, *Ulva* and *Codium* are usual. The bivalve *Brachiodontes* may occur as a byssate crust; other mollusca present but not common are *Tectus mauritianus*, *Vasum turbinellus* and *Pleuroploca trapezium*. The sublittoral zone is marked by the appearance of *Thalassia*, *Halodule* and *Cymodocea* which form extensive beds across the shallow sublittoral platform.

(ii) *Anse Porche* (grid reference 14480, 12600)

The cliff profile and the degree of undercutting here on the north shore of Middle Island is similar to that seen at Anse Var. The zonation of organisms is also closely comparable to that at Anse Var. Slight differences such as the presence of the limpet *Cellana cernica* low on the shore and abundant *Lithotrya* are probably local variations. At a more sheltered site well within the bay the eulittoral biota is less diverse and abundant but is marked by the presence of *Nerita polita* which uses the sandy beach as a subhabitat.

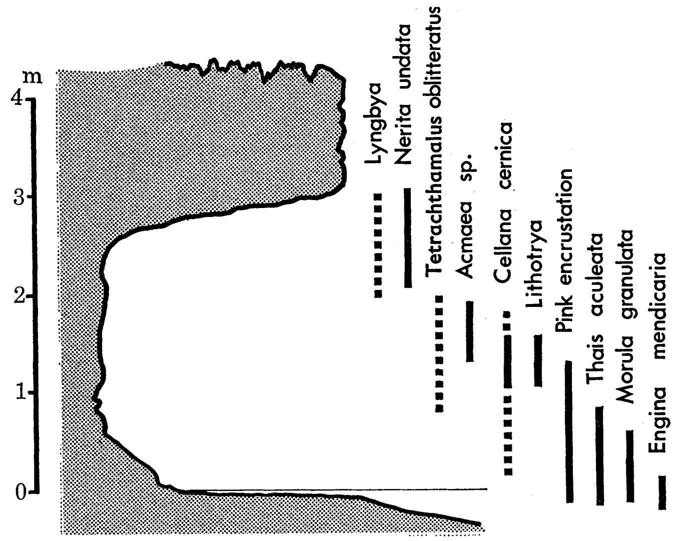

FIGURE 2. Zonation of intertidal organisms on cliff at Anse Porche (14480, 12600).

(iii) *Beach-rock on Picard* (grid reference 05560, 10080)

The beach-rock at the Settlement on Ile Picard is the most extensive development of this category of rocky shore around the atoll, and forms one of the few occurrences of shallowly sloping rock substrate. The rock dips seawards as a series of overlapping layers with small escarpments on the landward sides (figure 3). The higher portions are much pitted but the lower areas are relatively smooth but creviced. The exposure is about 30 m wide but it may experience frequent incursions of sand especially at the southern end. The presence of the sand may be of season duration which accounts for the depauperate flora and fauna found on the southern sector of the beach-rock.

Zonation of organisms on the beach-rock was studied along two transects and the general ranges of the major organisms is shown in figure 3.

The littoral fringe is occupied by *Littorina glabrata* and *Nerita plicata*. Both are active immediately after high water but retreat into clusters in depressions and crevices during the daytime at low water. *Nerita* prefers slightly damper and more shady sites than *Littorina*. The rock in this zone is coated with blue-green algae upon which the herbivorous gastropods feed.

The top of the eulittoral zone is marked by the presence of *Tetrachthamalus oblitteratus*, and *Siphonaria madagascarensis*, the chiton *Acanthopleura* was not common on the beach-rock. *Tetrachthalamus* ranges about half way across the beach-rock and is eaten by the gastropods *Thais aculeata* and *Morula granulata*. A little lower the green alga *Enteromorpha* is associated with short growths of *Ulva* which form a distinct band on the shore. There seems to be some seasonal control on the growth of these algae, for in the calm season the band is much more conspicuous than during the time of the southeast trades.

Low in the eulittoral a subzone is formed by the mytilid bivalve *Brachiodontes variabilis* which occurs in tight byssate masses occupying an area about 11 m wide. Together with the bivalves there is a crust formed by coiled chitinous tubes of eunicid worms. Algae such as *Ulva*, *Turbinaria* and encrusting calcareous red algae occur on and between the bivalve crust. Associated with the mussel and eunicid belt are the gastropods *Morula granulata* and *Conus ebraeus* which feed upon *Brachiodontes* and eunicid worms respectively.

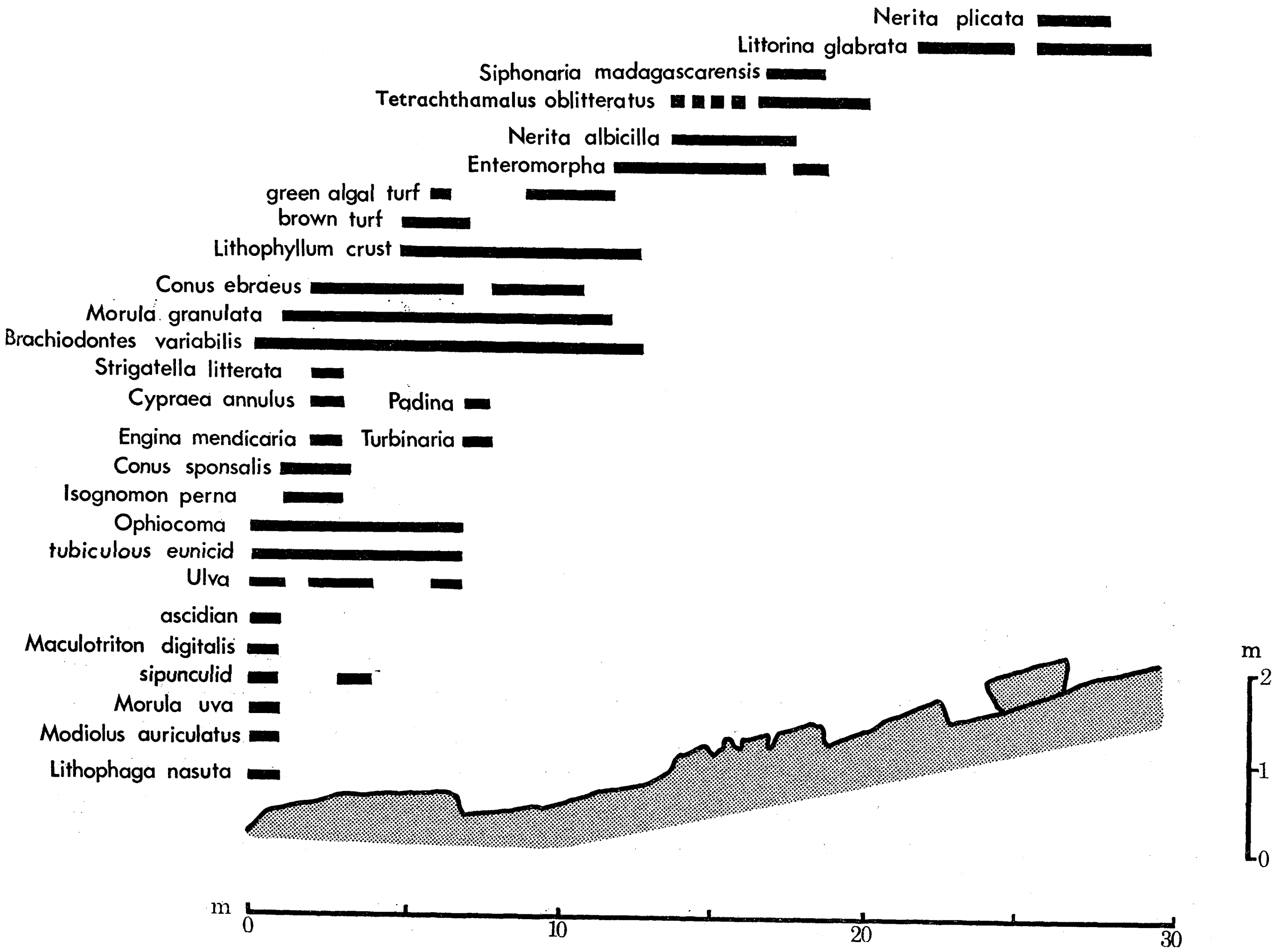

FIGURE 3. Beach-rock on Picard (05560, 10080) showing zonation of intertidal organisms.

On the lowest levels of the beach-rock which project into the sublittoral fringe the fauna and flora is much more diverse and contains species which occur all over the sublittoral platform. Most of these animals remain in crevices during low tide and include large numbers of the ophiuroid *Ophiocoma brevipes*, byssate bivalves such as *Isognomon perna*, *Barbatia decussata*, the gastropods *Engina mendicaria*, *Cypraea annulus*, *Conus sponsalis* and *Maculotriton digitalis*. Xanthid crabs such as *Leptodius sanguineus* and *Xanthias lamarcki*, pagurids such as *Calcinus laevimanus* and the anomuran *Petrolisthes lamarcki* are abundant. Larger crabs such as the predatory *Eriphia laevimana* and *Grapsus tenuicrustatus* are common in mid and upper shores respectively.

The rock of these lower portions is riddled with the holes of boring polychaetes, sipunculids, sponges, *Lithotrya* and the bivalve *Lithophaga nasuta*.

(iv) *East Channel seaward shore* (grid reference 30730, 12330)

Shores with rather higher exposure factors than Anse Var and Anse Porche such as the seaward shore near East Channel are less undercut and frequently are vertical or slope steeply landwards (figure 4). Cliff falls appear to be frequent here and it apparently represents a shore transitional in energy between the ramp-like cliffs of the exposed coasts and the undercut cliffs of sheltered shores.

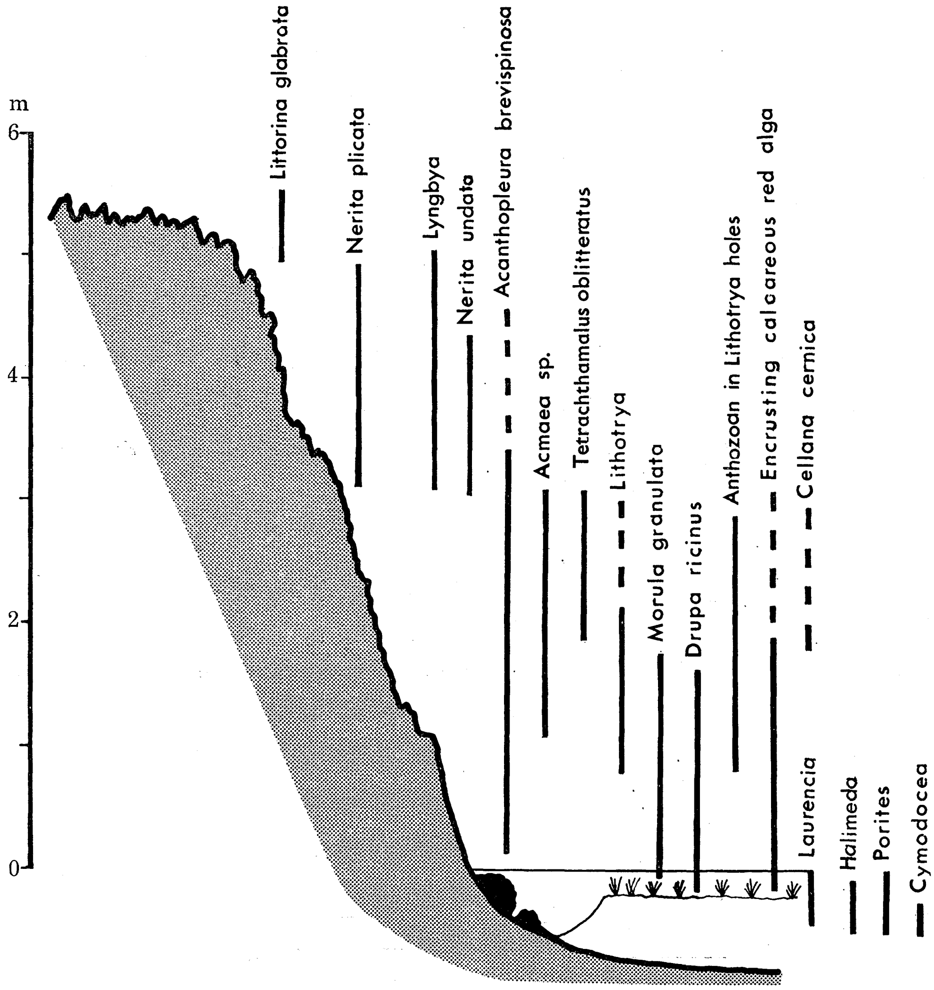

FIGURE 4. Intertidal zonation on cliffs at East Channel, north side, seaward (30730, 12330).

The zonation pattern is essentially similar to that of sheltered shores but the fauna of the low eulittoral is more diverse and abundant. With the exceptions of blue-green algae crust, macroscopic algae are rare in the high and mid-eulittoral. *Tetrachthamalus* is uncommon but the boring barnacle *Lithotrya* forms a distinct belt. The most common limpet is *Acmaea* which is exceedingly common in the small pitted crevices of the limestone surface. Lower, *Cellana cernica* is present but uncommon. At the base of the cliff gastropods *Strigatella litterata*, *Vasum turbinellus*, *Thais aculeata*, *Drupa margariticola* are common, and in the larger crevices *Turbo marmoratus* may occur. The nudibranch *Onchidium* sp. occurs low on the cliff faces, the black colour and shape closely resembling *Acanthopleura*.

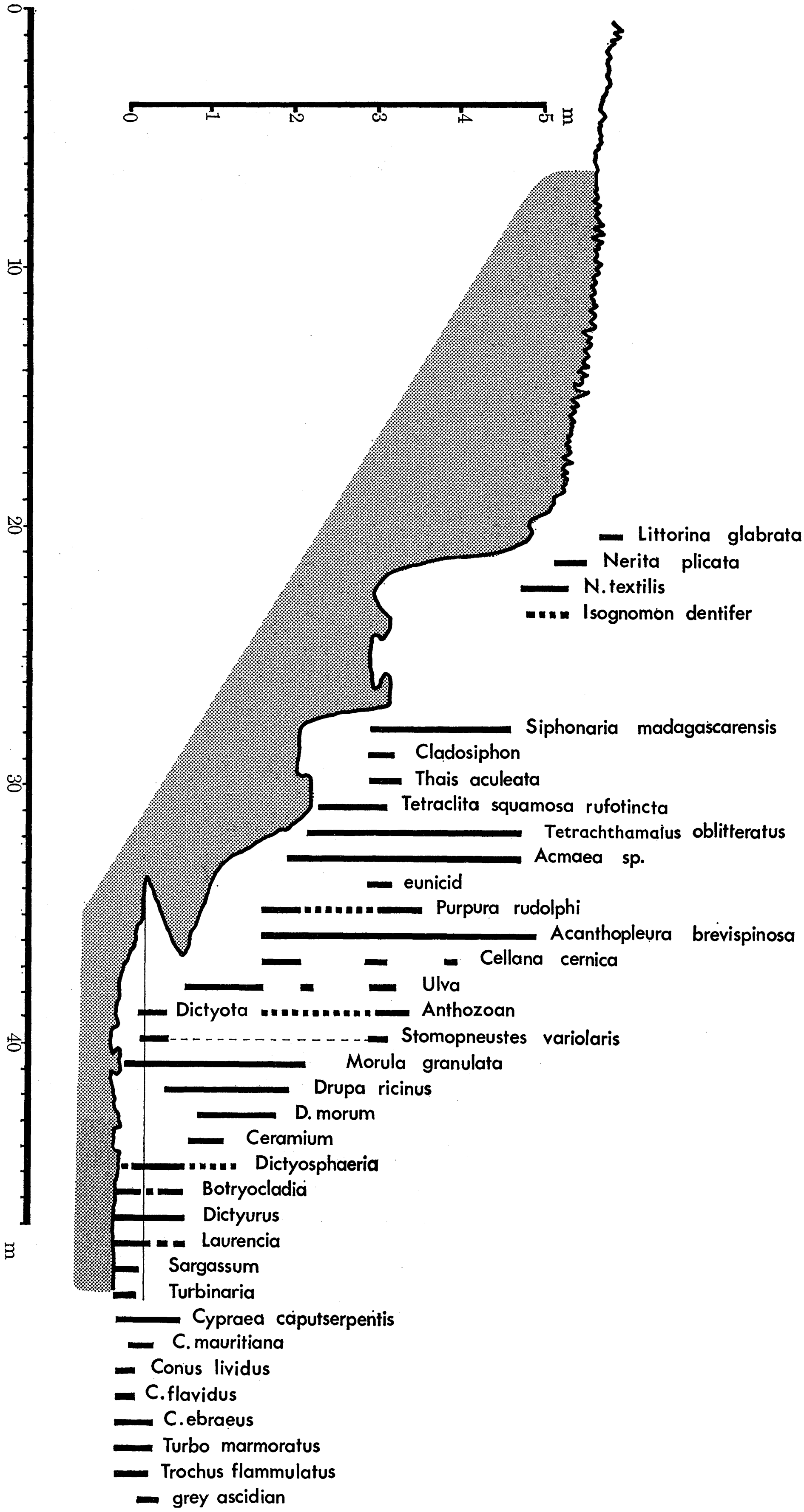

FIGURE 5. Zonation of organisms on cliff at Dune d'Messe, seaward (19180, 10210).

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At the base of the cliff there is a moat with standing water up to 1 m deep which contains corals such as *Porites lutea*, *Goniastrea*, *Favia*, *Millepora platyphylla* and *Cyphastrea* cemented to the rock surface. Algae such as *Laurencia*, *Halimeda* and *Turbinaria* are common. The bottom of the moat is usually occupied by loose dead coal cobbles sometimes encrusted with calcareous red algae such as *Peyssonelia*. The seaward side of the moat rises gradually up to the *Cymodocea*-covered seaward platform.

(*b*) *Exposed shores*

Along the south and east of the atoll the shores are exposed to the dominant southeast trade winds for a good part of the year. The cliff profiles and the zonation of organisms upon them are markedly different to those seen on more sheltered shores.

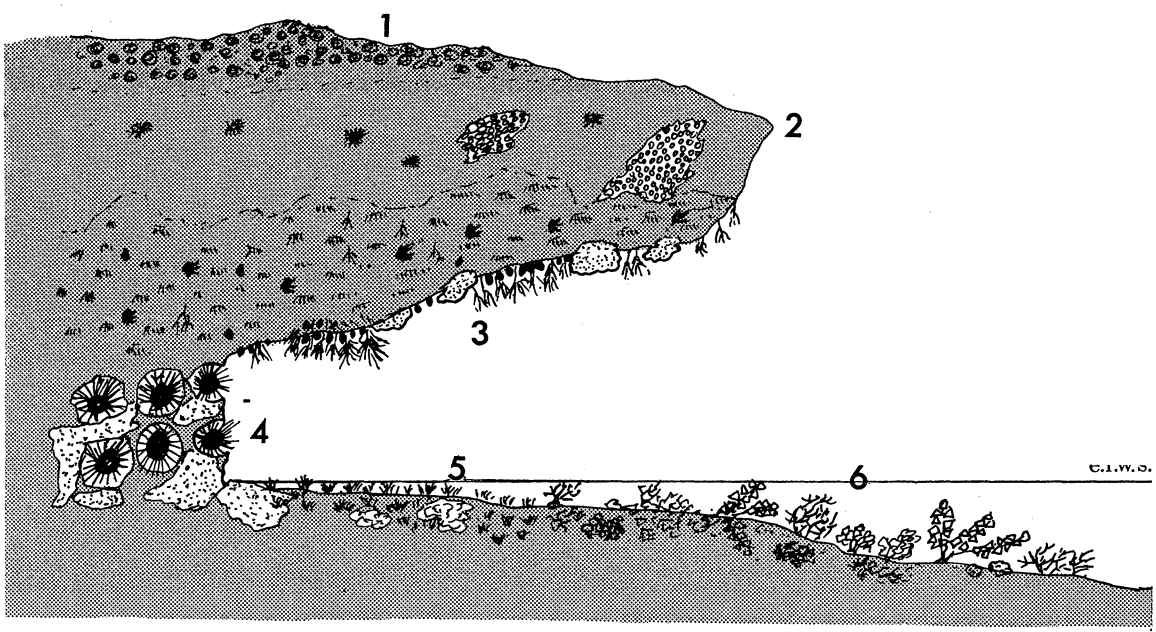

FIGURE 6. Diagrammatic representation of zonation in the undercut at the sublittoral fringe at Dune d'Messe. 1, Tubiculous eunicid worm, *Morula granulata* and *Drupa ricinus*. 2, Zoanthid, *Cladophoropsis*, *Dictyosphaeria*, *Drupa ricinus*. 3, *Dictyurus*, *Botryocladia*, sponges, hydroids, and ascidians. 4, *Echinometra matthaei*, *Stomopneustes variolaris*, colonial ascidians, *Cypraea caputserpentis* and *C. mauritianus*. 5, '*Gelidium*' turf, *Cladophoropsis*, *Pocockiella* and tubiculous eunicid worms. 6, *Turbinaria*, *Codium*, *Halimeda*, '*Gelidium*' turf, *Conus* species.

(i) *Dune d'Messe* (grid reference 19180, 01210)

Here the cliff is 5 to 6 m high and the width from the perched beach to the base of the cliff at the sublittoral platform is 35 to 45 m. At the landward edge the cliff consists of a gently sloping platform about 20 m wide. The limestone on this platform is scoriaceous, grey, with small sand pockets; although continuously affected by salt spray it is washed by waves at the highest spring tides. As the steep seaward edge of the cliff is reached small flat-bottomed pools occur containing standing water, these may be up to 1 m in diameter. At the cliff edge the pools become more deeply incised and the surrounding pinnacles higher. The rock is here brown coloured. The cliff then descends steeply in a series of rimmed pools to about 1 m above l.w.s. where it flattens out into a ledge which is projected seawards in a series of spurs which are separated by deep groves, gullies and scour holes. The 1 m ledge shows undercutting to a depth of about 1 m at the seaward extremity at the l.w.s. level. Seawards of this the sublittoral platform extends at a fairly uniform level about 0.5 m below l.w.s.

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Zonation. At the extreme landward portion of the cliff *Littorina glabrata* occurs but is nowhere common. Except for a blue-green algal coating to the rock most of the rest of the flat cliff top is bare of life. At the seaward edge of the high platform where standing water is present in pools *Nerita plicata* and a little lower *N. textilis* occur. The byssate bivalve *Isognomon dentifer* is found in damp crevices at this level.

As usual the top of the eulittoral zone is marked by the occurrence of *Tetrachthamalus*, *Acmaea*, *Siphonaria* and *Acanthopleura*. These appear on the highest portions of the steep cliff face. The highest of the tide pools is occupied by stringy growths of the alga *Cladosiphon*, and the ophiuroid *Ophiocoma brevipes* occurs in crevices, other pools at this level may also contain *Ulva* and the boring echinoid *Stomopneustes* which forms an undercut rim to the pool. On the rocks surrounding the pool *Cellana cernica* and the predatory gastropods *Thais aculeata* and *Purpura rudolphi* occur. On the steep slope joining the pool levels a second larger barnacle *Tetraclita squamosa rufotincta* is found; *Tetrachthalamus* is at this level fairly sporadic. *Tetraclita* is eaten by *Purpura rudolphi*. The pools at the lower level are fairly well scoured and only sporadic *Ulva* and *Cladosiphon* are present. Below this level of pools there is a broad belt about 1.5 to 2 m above l.w.s., dominated by the green alga *Ulva* which may be projected up into higher shore levels along surge channels. This *Ulva* belt is approximately 1 m in width and it is succeeded lower on the shore by a belt about 0.75 m in width which consists of a short turf of algae including *Ceramium*, *Gelidium* and *Dictyosphaeria*. On these two lower levels the predatory gastropods *Morula granulata*, *Drupa morum* and *D. ricinus* are common.

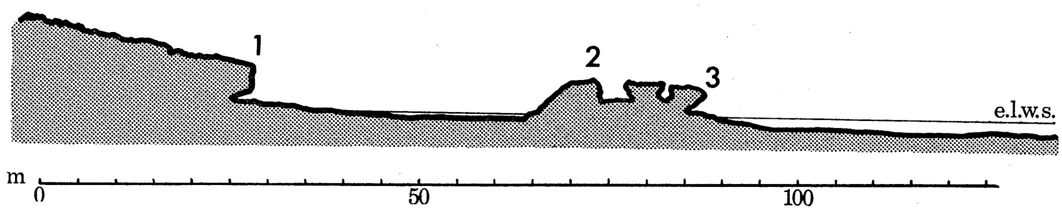

FIGURE 7. Diagram of shore profile at Dune Jean-Louis (26350, 03560) showing sites to which figures 8 to 10 refer.

The undercut beneath the lowest ledge of the projecting spurs shows a very different and very diverse biota (figure 6). The roof of the undercut is coated with red algae *Dictyurus* which hangs in short festoons, and *Botryocladia* closely epilithic in grape-like growths and the finely branching calcareous *Jania*. The actual notch is formed and occupied by the echinoids *Stomopneustes variolaris* and *Echinometra matthaei* which excavate hemispherical burrows by rotatory action. The rock surface between the cavities is coated by encrustations of calcareous red algae, pads of a grey colonial ascidian and sponges. The floor of the undercut may be occupied by masses of a chitinous tubed eunicid worm, ascidians, sponges and algae such as *Halimeda*, *Dictyota*, *Gelidium*, *Turbinaria*, *Codium*, *Laurencia* and the byssate bivalve *Modiolus auriculatus*.

The shaded notch is the habitat of several large gastropods such as *Turbo marmoratus*, *Cypraea mauritiana*, *C. arabica* and *Tectus mauritianus* and others such as *Cypraea caputserpentis*, *C. helvola* and *Trochus flammulatus* occupy abandoned echinoid holes. The base of the notch is covered by an algal turf but it is much creviced and loosely cemented limestone blocks are common. In the crevices and beneath the blocks and in the algal turf a very diverse fauna is found. Common gastropods are species of *Conus*, *C. coronatus*, *C. catus*, *C. ebraeus*, *C. rattus*, *C. flavidus*, *C. lividus*, *Vasum turbinellus* and *Bursa granularis*.

Boring into the limestone blocks are abundant nereid, eunicid and sipunculid worms. *Eurythöe* is common beneath the blocks, and in the small sand pockets beneath blocks ptychoderid worms occur. Ophiuroids, particularly *Ophiocoma erinaceus*, and the holothurians *Afrocucumis africana*, *Holothuria pardalis* and *H. cinerascens* are common.

(ii) *Dune Jean-Louis* (grid reference 26350, 03560)

At Dune Jean-Louis the almost continuous ramp-like cliffs of the south coast are breached and small sandy beaches backed by dunes are present. The cliff line between these beaches shows a slightly different profile to the rest of the south coast and it appears as if cliff retreat has proceeded at a faster rate here.

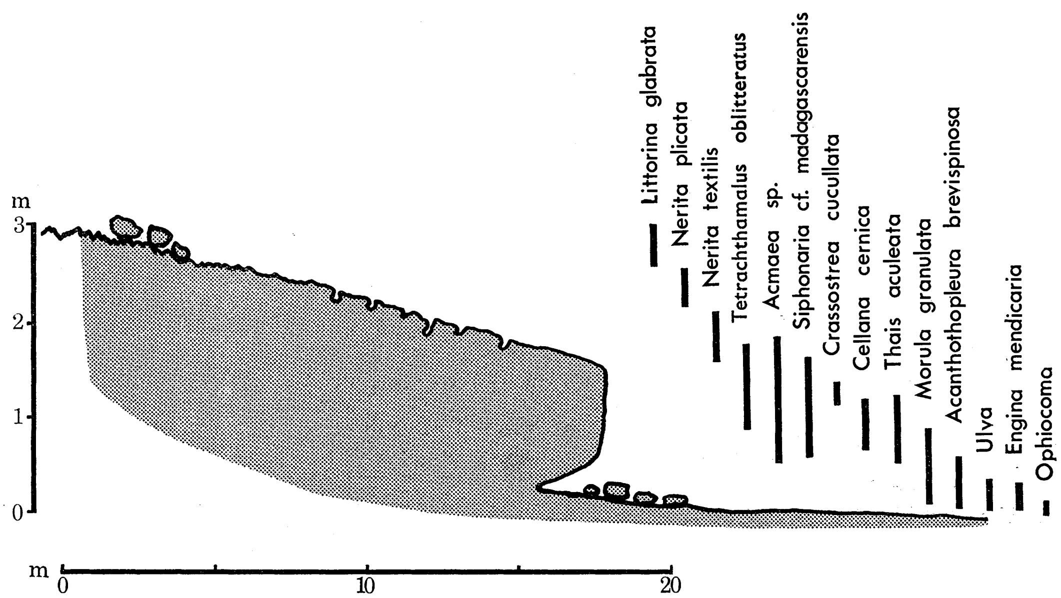

FIGURE 8. Zonation of organisms on cliff at Dune Jean-Louis.

The landward portion of the cliff is similar to that found elsewhere except that because of a beach-rock capping, the surface is generally smoother and the seaward portion more dissected by smooth-sided pot-holes (figure 8). The cliff is terminated to the seaward by a more or less vertical cliff about 2 m high at the base of which is a small undercut and many loose limestone blocks. The undercut lies at about m.l.w. From the cliff a platform extends for about 40 m seawards with fairly low topography and then rises up to remanié masses of limestone with an average height of 1.5 to 2 m but rising to 3.2 m above the platform. These residual masses are dissected by pools and gullies and surrounded by an undercut notch at the e.l.w.s. level. The notch is deeper on the seaward than landward side. Seawards the platform extends for another 100 m at a shallow sublittoral level.

The fauna of the higher shore is essentially similar to that seen at Dune d'Messe except that as the cliff top level is somewhat lower *Nerita plicata* and *N. textilis* range over most of its surface, with the extreme landward portion occupied by *Littorina glabrata*. The steep seaward cliff face is colonized by the usual eulittoral species but including *Crassostrea cucullata*. Lower on the cliff face an *Ulva* and *Ceramium* belt is present. Beneath the boulders at the base the gastropods *Engina mendicaria* and *Morula granulata* and the ophiuroid *Ophiocoma brevipes* are abundant.

The upper parts of the residual limestone masses (figure 9) are colonized by abundant *Tetraclita squamosa rufotincta*, *Cellana cernica* and *Acanthopleura*. In the pools with standing water *Stomopneustes* and *Echinometra* have intricately dissected the sides and bottoms; the alga *Sargassum* is attached to the sides in long strands and *Dictyurus* and *Botryocladia* form a shorter turf. At the bottom of the pools *Halimeda* and *Codium* are common with a short *Gelidium* turf. Some encrusting corals such as *Favia*, *Porites* and *Cyphastrea* occur. At the seaward faces of the residual cliff the organisms described for this habitat at Dune d'Messe are present (figure 10).

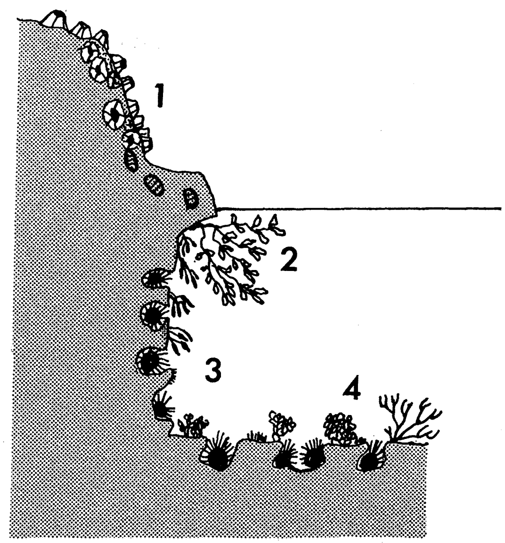

FIGURE 9. Diagrammatic representation of zonation on the side of an intertidal pool on a remanié limestone mass at Dune Jean-Louis. 1, *Tetraclita squamosa rufotincta* and *Acanthopleura brevispinosa*. 2, *Sargassum* and *Dictyurus*. 3, *Echinometra*, *Stomopneustes*, *Dictyurus* and *Gelidium*. 4, *Echinometra*, *Stomopneustes*, *Halimeda*, *Codium* and '*Gelidium*'.

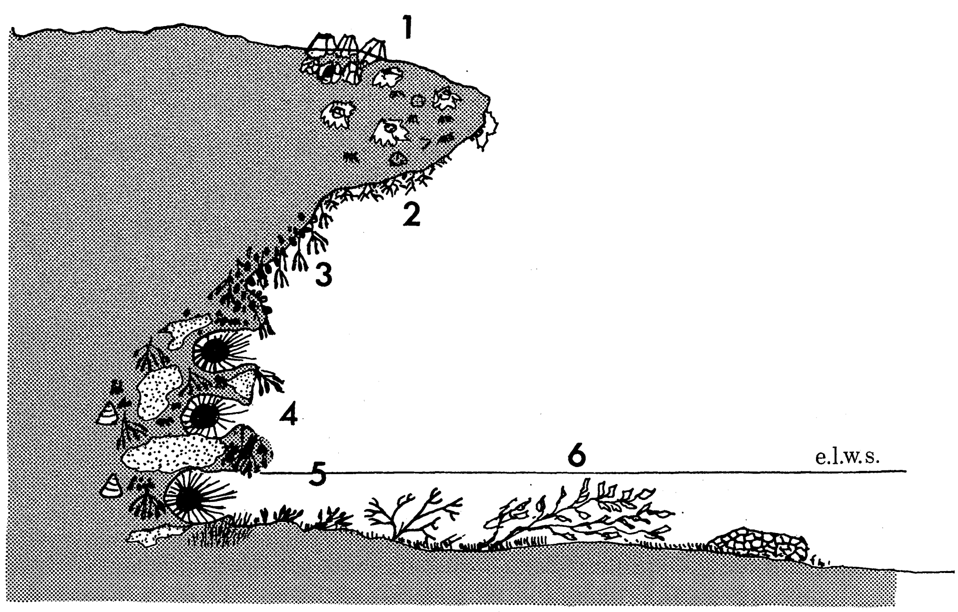

FIGURE 10. Representation of zonation in the sublittoral fringe notch at Dune Jean-Louis. 1, *Tetraclita squamosa rufotincta*, *Cladophoropsis*, *Drupa ricinus*. 2, *Cladophoropsis* and *Botryocladia*. 3, *Botryocladia*, *Dictyurus* and sponges. 4, *Echinometra*, *Stomopneustes*, *Dictyurus*, colonial ascidians and *Trochus flammulatus*. 5, *Dictyurus*, '*Gelidium*' and tubiculous eunicids. 6, *Sargassum*, *Codium* and coral.

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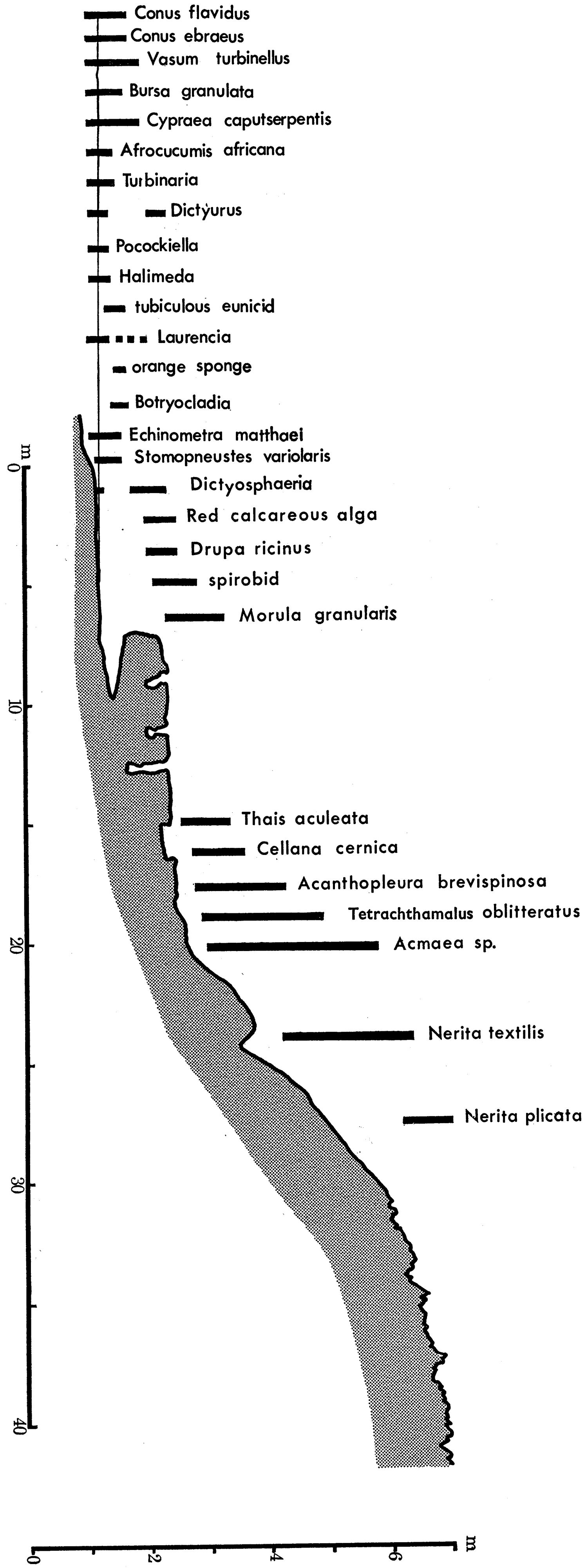

FIGURE 11. Intertidal zonation at Cinq Cases (39630, 05500).

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(iii) *Cinq Cases* (grid reference 39630, 05500)

The cliff here (figure 11) can be divided into two levels with the narrow sublittoral platform constituting a third.

The landward portion of the cliff is again flat topped but the small-scale topography of the surface is very dissected and scoriaceous. This level is about 20 m wide and blackened by blue-green algae.

This is followed seawards by a steep descent with many solution pools with a hint of a break in slope about half way down at the high-water neaps level. This platform is dissected by pools up to 0.75 m deep and at the outer edge small channels. The platform is however fairly uniformly level, and is terminated seawards by a small cliff about 1 m high, with a deep undercut notch leading to the sublittoral platform.

Zonation. Again the higher intertidal fauna is very similar to that seen at other sites around the exposed south shore. *Nerita textilis* is very abundant around the high pools. *Acanthopleura*, *Tetrachthamalus* and *Acmaea* are all present at the top of the eulittoral. At the lower part of the steep face the limpet *Cellana cernica* and the muricid gastropod *Thais aculeata* are common. *Tetraclita squamosa rufotincta* is found in this situation but not on this transect.

The mid-littoral platform is thickly coated by encrusting calcareous red algae, giving it a distinct pink appearance. Within this crust a small coiled tube eunicid worm is common. Apart from this the upper platform surface is very bare and it is only in the pools dissecting the platform and in the channels that any diverse flora and fauna are developed. In the pools the algae *Turbinaria*, *Laurencia* are common and in some pools corals such as *Goniastrea*, *Porites* and *Favia* occur in encrusting growths. Some of the pools have sand trapped in them and the sand supports a fauna of ptychoderid worms, sipunculids, burrowing holothurians such as *Holothuria arenicola* and the occasional bivalve. The predatory gastropods *Morula granulata* and *Drupa ricinus* are the only molluscs common on the upper surface of the platform.

The undercut notch at the seaward edge of the platform is, as at other southerly sites, cut by the echinoids *Stomopneustes* and *Echinometra*. Hanging from the roof of the notch is a turf of the algae *Dictyurus*, *Botryocladia* and hydroids, which is thicker here than at other sites. The pads of the grey ascidian in the notch are also more abundant than at other sites.

The floor of the undercut notch is occupied in the shady parts by *Dictyurus* in rather more stumpy growths than on the roof and *Pocockiella*, which passes into a turf of *Laurencia*, *Cladophoropsis*, *Dictyosphaeria*, *Turbinaria*, *Halimeda* and *Gelidium*. This sublittoral fringe turf and the crevices in the rock platform beneath it are occupied by the very diverse fauna similar to that described for other south coast sites.

(iv) *Point Hodoul* (grid reference 40600, 09020)

This site experiences the most severe exposure conditions on the atoll.

The sublittoral platform which was narrow at Cinq Cases has now almost disappeared (figure 12) and the mid-littoral platform falls off steeply with a cliff about 4 m high onto a narrow platform, dissected by surge channels, which descends into deeper water. The higher portions of the cliff are morphologically similar to those described at Cinq Cases but the steep fall down onto the mid-littoral platform is much dissected. The mid-littoral platform is about 15 m wide, fairly level but dissected by pools and channels at the edge.

Zonation. The higher fauna is similar to that described for other exposed sites, *Tetraclita* is

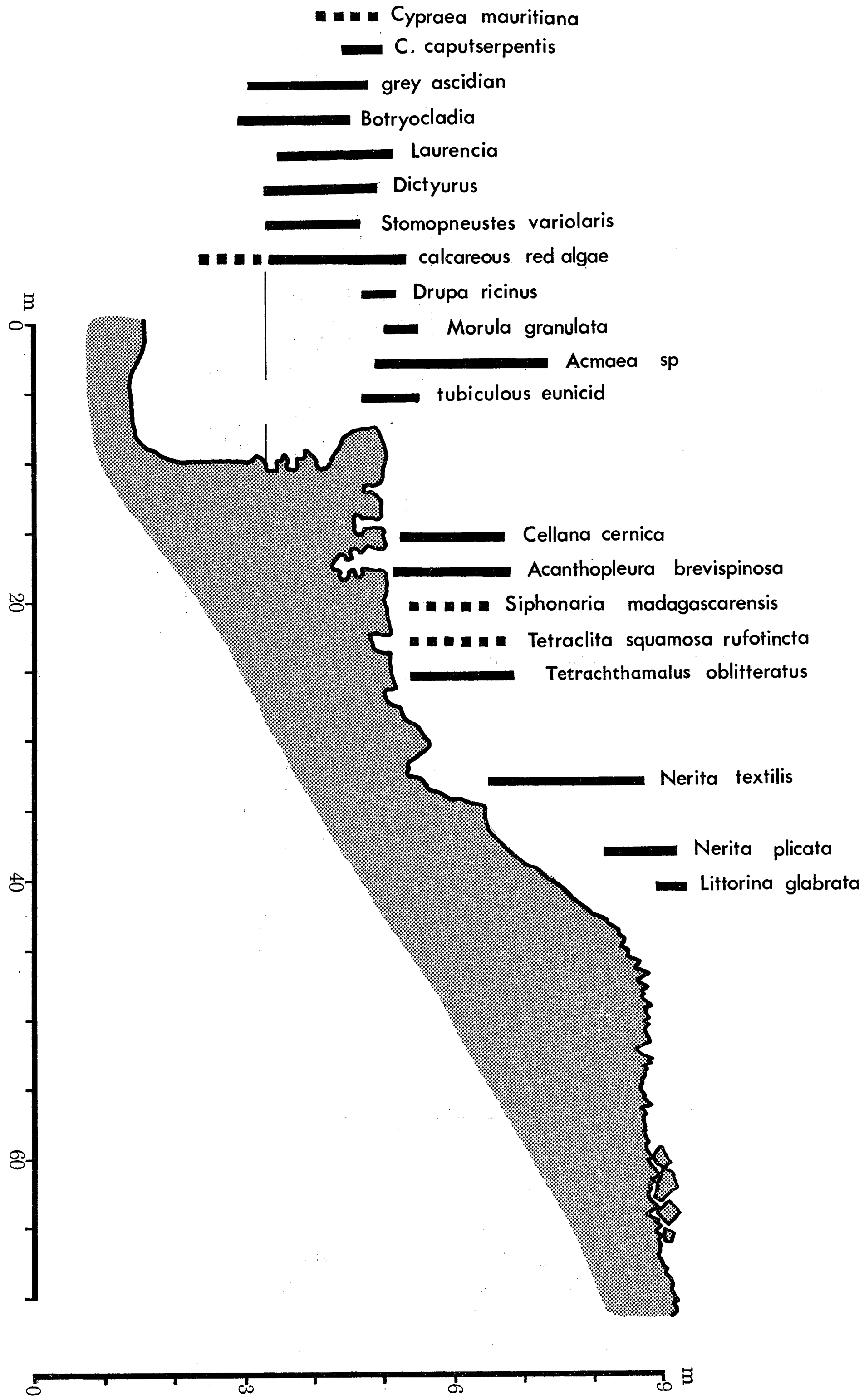

FIGURE 12. Zonation of intertidal organisms at Point Hodoul (40600, 09020).

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abundant on the lower portions of the steep face of the eulittoral cliff. The mid-littoral platform is very heavily encrusted by pink calcareous algae and eunicid worms. Mollusca common on the open platform include *Morula granulata* and *Drupa ricinus* which feeds upon the eunicids. The limpet *Acmaea* is common and the nudibranch *Onchidium* is present on open surfaces.

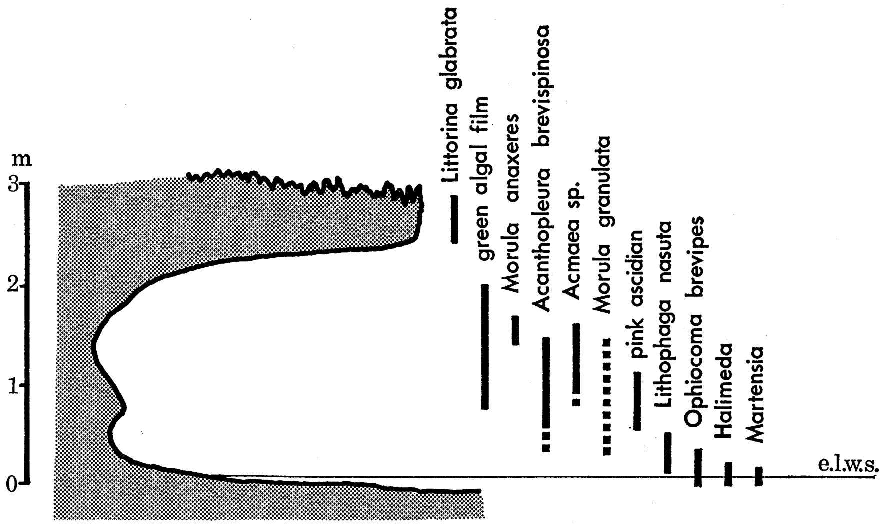

FIGURE 13. Zonation of organisms on cliff on the west side of East Channel (3140, 1200).

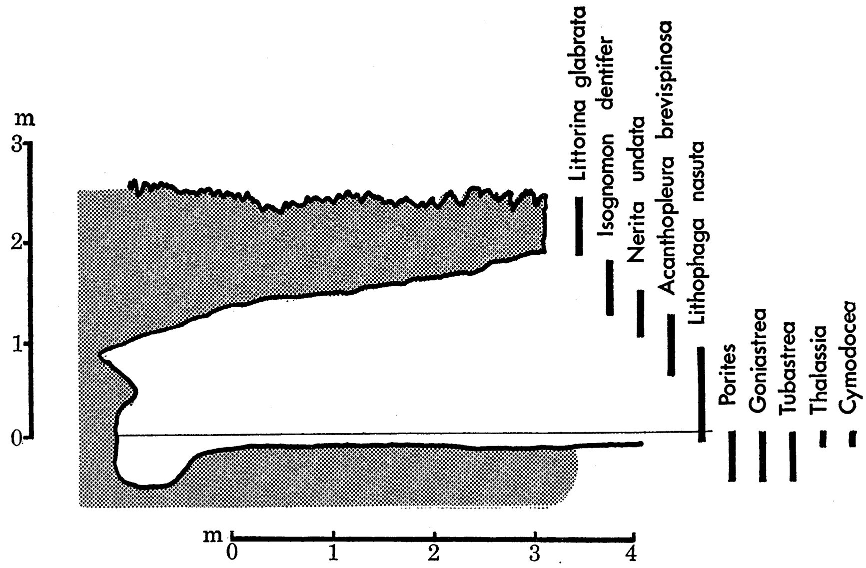

FIGURE 14. Intertidal zonation upon the north side of a lagoon islet south of East Channel (3152, 1054).

The rock pools are largely flat bottomed but dissected by the cavities of boring echinoids. The rest of the pools are clothed in an algal cover of *Dictyurus*, *Laurencia*, *Cladophoropsis*, *Caulerpa* and *Halimeda*. The algal flora is more abundant and diverse at the seaward edge of the platform, the landward pools containing *Laurencia* alone. The mollusca *Turbo marmoratus*, *Tectus mauritianus*, *Cypraea mauritianus* and *C. caputserpentis* are typical of the pools.

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At the seaward edge of the platform there are abundant cushions of bright pink *Laurencia*, and beneath the slight undercut *Dictyurus*, *Botryocladia* and *Cladophoropsis* are as usual abundant together with the pair of boring echinoids and the grey colonial ascidian.

The algal flora in the eulittoral at this site is more abundant and diverse than at any other intertidal site.

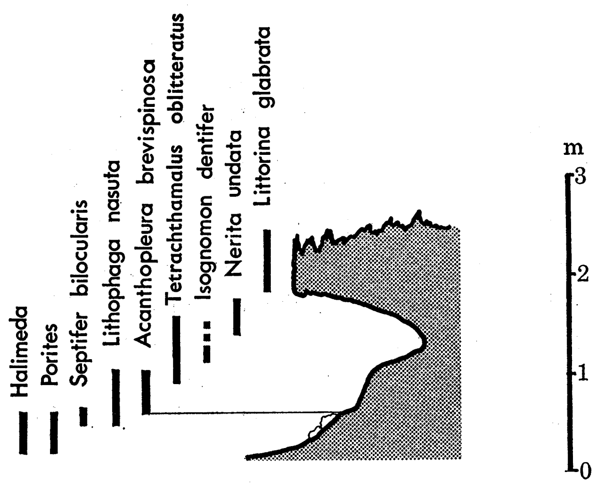

FIGURE 15. Zonation of organisms on the west face of an islet in Passe Femme, West Channels (06100, 06800).

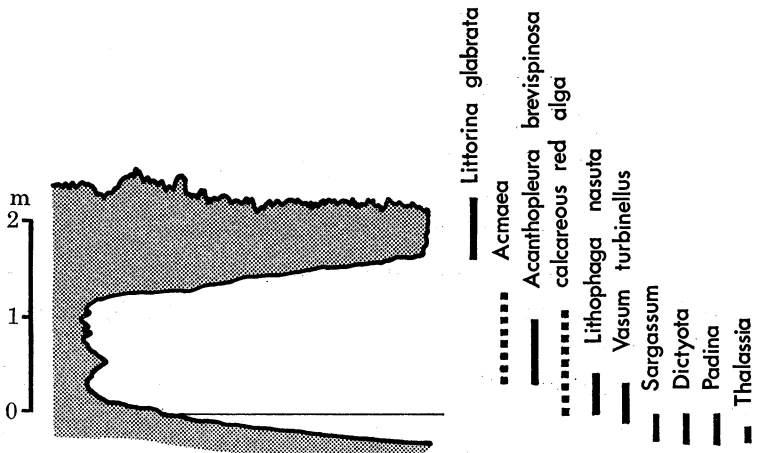

FIGURE 16. Intertidal zonation on the southwest face of a lagoon islet in Passe Femme (06600, 09200).

(*c*) *Channels*

The cliffs in channel areas show a transitional morphology and zonation pattern from the seaward sites to the lagoon (figures 13 to 16). These areas are subjected to regular tidal interchange of water between the lagoon and the open sea. Consequently currents are strong and circulation is better than on sheltered seaward shores but not as good as on exposed shores. The zonation in channel areas shows certain special characteristics. The cliffs are sheltered and the height of the cliffs decreases and the depth of undercut increases when compared with seaward sites. Wave action is low so that the width of the littoral fringe and the zonation in the fringe and in the eulittoral is essentially similar to that seen on sheltered shores. Certain differences are apparent, for instance *Nerita plicata* is uncommon, but the oyster *Crassostrea cucullata* is abundant in the mid-eulittoral and *Chama imbricata* in the low eulittoral. *Isognomon dentifer* is common in byssate clumps above the undercut and is more abundant in channel areas than at any other site. *Nerita undata* is typically found beneath the shaded overhang and *Lithophaga nasuta* is abundant low in the eulittoral and sublittoral.

It is in the lowest eulittoral and sublittoral fringe that the greatest distinctiveness of the channel areas can be seen. The good circulation and shorter emersion times immediately adjacent to the channels mean that corals can survive at the base of the cliffs in the low eulittoral. These corals are usually encrusting species such as *Montipora*, *Cyphastrea*, semi-encrusting such as *Porites* and *Millepora*, or branching such as *Porites nigrescens*. Such corals could be seen in the deeper moat at the base of the cliff at certain sites. However, it is only in channel areas that the ahermatypic corals, the black *Dendrophyllia* and the orange *Tubastrea* and the small solitary *Paracyathus*, are found in shallow water areas. The more usual habitat of these species is in the deeper water of the sublittoral. In all the channels these species are seen attached to the base of the cliffs and may be subjected to emersion and the sites in which they occur are usually shaded for much of the day and where they occur in unshaded sites they are in positions of strong waterflow.

Associated with the corals at the base of the cliffs are sponges encrusting the rock surface or interpenetrating the coral branches or beneath coral colonies. Many species of hydroids are found. Encrusting calcareous red algae are common as are *Halimeda*, *Caulerpa*, *Laurencia* and *Polysiphonia*. Within the coral and sponge masses is a great diversity of mollusca and echinoderms including the sponge-feeding gastropods *Cypraea carneola*, *C. imbriata* and several species of byssate bivalves such as *Barbatia helblingi*, *Pinctada margaritifera*, *Cardita variegata*, *Isognomon perna*. Ophiuroids such as *Ophiocoma erinaceus*, *O. valenciae*, *Ophiolepis cincta*, *Ophiactis savignyi* and the echinoids *Echinometra matthaei* and *Diadema savignyi* are abundant.

(*d*) *Lagoon shores—extreme shelter*

At the lagoon shore of Dune d'Messe (grid reference 18530, 02950) for example the cliff is less than 2 m high with an undercut notch of more than 3 m in depth. However, all transitional stages are seen but in general the cliffs surrounding the lagoon are less than 3 m in height. Residual islets are common around the lagoon margins. Most of the lagoon shore is fringed by mangroves which form a complex mosaic with the dissected cliff, solution holes and residual islets. Dissection of the cliff is in general more severe when covered by mangrove growth.

The southern shore is shallower than the north side. To the south there is a broad intertidal platform up to 700 m wide, formed by the retreat of the cliffs, which slopes gradually lagoonwards. The surface of this platform is dissected into broad subcircular depressions up to about 2 m in diameter, with frequently a sediment fill of fine grey sand. The intervening ridges are usually bare rock surfaces but may have a thin sediment crust fixed by blue-green algae. This intertidal platform is essentially similar in character from Moustique to Takamaka Passage.

The zonation pattern at Dune d'Messe lagoon shore may be taken as typical for the southern lagoon shore. The fauna and flora for the intertidal cliff is shown in figure 17. It is very sparse with only a few *Isognomon dentifer* and *Nerita undata* immediately beneath the undercut, with blue-green algae. The faunal elements typical of the eulittoral *Siphonaria*, *Tetrachthamalus* and *Acanthopleura* appear low in the undercut notch and range across the inshore part of the basal platform. Confined to the low eulittoral on the basal platform but ranging up to the bottom of the cliff is the herbivorous gastropod *Cerithium morum* which is exceedingly common.

On the flat intertidal platform extending into the lagoon (figure 18) there occurs in the area up to 30 to 40 m from the mangrove fringe or the limestone cliff a fauna typical of the mangrove fringes. The large gastropod *Terebralia palustris* occurs among the roots of mangroves but also upon more open substrates where it feeds upon the algal film of sediment surfaces. The fiddler crab *Uca tetragonon* inhabits burrows which penetrate the sediment cover into the underlying dissected limestone surfaces both on the open platform and between the mangroves. The

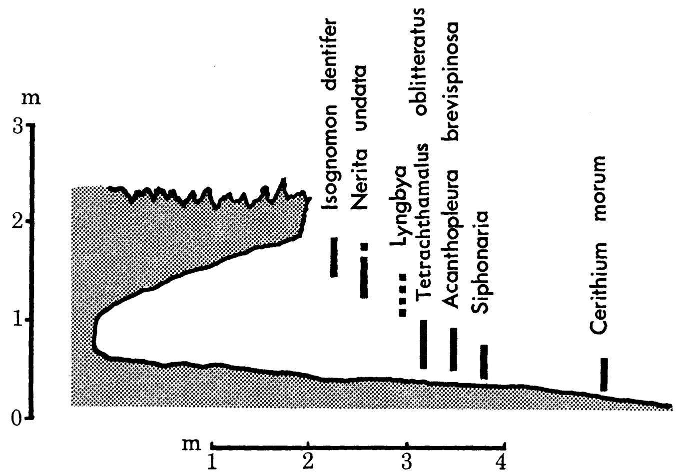

FIGURE 17. Zonation of organisms on cliff on lagoon shore at Dune d'Messe (18530, 02950).

portunid crabs *Thalamita crenata* and *Scylla serrata* occur in the mangrove fringe, the former is very common inhabiting burrows in the bottoms of sediment depressions which are always water covered. The upstanding portions of the rock surface are coated with a blue-green algal crust. Lagoonwards the mangrove fringe species disappear and are replaced dominantly by *Cerithium morum* which occurs in vast numbers up to 1000 m^{-2} both on the rock and sediment pools and in the shallow pools. The alga *Enteromorpha* occurs on the sediment surface and a khaki crust of *Colpomenia* on the emersed rock surfaces. In slightly deeper pools other algae such as *Laurencia* occur.

Around 250 to 300 m from the shore small byssate clumps of the mytilid bivalve *Brachiodontes variabilis* occur attached to the ridges of rock between the pools. Lagoonwards these byssate clumps become more abundant and larger until at around 400 to 500 m from the shore they have fused to form sinuous ridges with densities of up to 7000 m^{-2}. With the increase in abundance of *Brachiodontes* there is a decrease in abundance of *Cerithium morum*. At around 400 m where the depth of standing water in the pools at low water is approximately 30 cm there is an increase in the number and abundance of algae present. *Ulva* is present on the rock ridges and *Acanthophora*, *Halimeda*, *Laurencia* and *Ceramium* are common in the pools. The holothurian *Halodeima atra*, and sponges appear in the pools and together with the algae listed above are common all across the lagoon. The sponges contain the commensal bivalve *Vulsella vulsella*.

The zonation pattern described for the broad intertidal platform at Dune d'Messe is essentially similar along most of the southern shore of the lagoon. However the byssate masses of *Brachiodontes* appear restricted to the southwestern part of the lagoon.

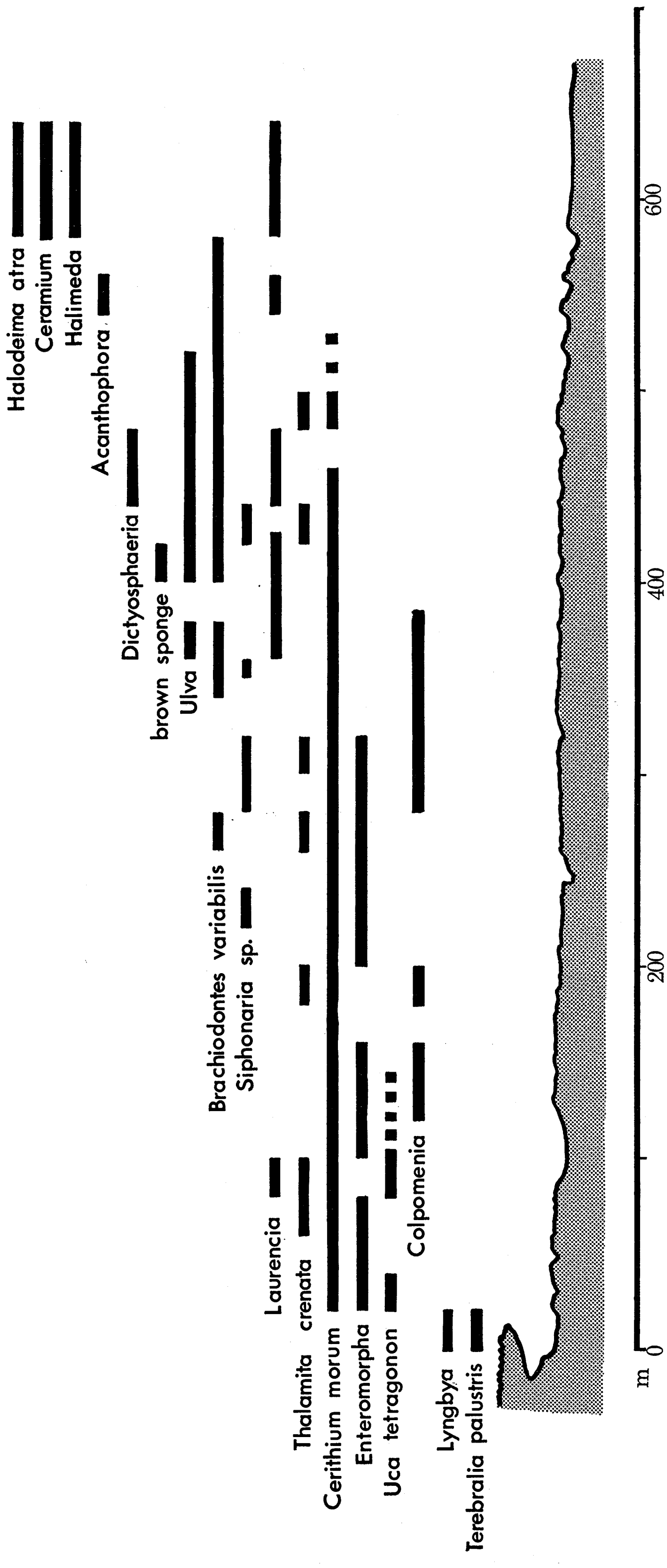

FIGURE 18. Zonation of organisms on the intertidal platform on the southern shore of the lagoon at Dune d'Messe (18530, 02950).

The northern shore of the lagoon is covered by a greater depth of water than the southern shore. The base of the cliff is not normally emersed at low water and the rock bottom with the thin sediment cover is usually covered by at least 0.5 to 1 m of water at low tide. This northern shore is exposed to wind-waves developed across the lagoon by the southeast Trades, consequently exposure is rather higher than the southern shore.

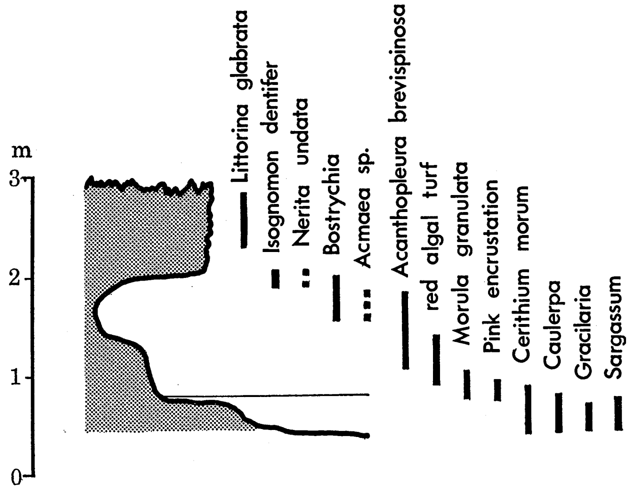

FIGURE 19. Intertidal zonation of organisms on the south face of Ile Verte on the northern shore of the lagoon (26230, 100300).

Along most of the northern shore the limestone cliffs are fringed by mangroves but on promontories and islets the zonation patterns may be seen. The pattern seen on the southern shore of Ile Verte (26230, 10300) (figure 19) may be taken as typical of the northern shore. Although the constituents of the fauna are similar to those at other sites they are distinctly more abundant than at sites on the southern shore. The appearance of algae such as *Bostrychia* in the high eulittoral and a dense algal cover in the low eulittoral is significant. In the shallow sublittoral of this north part of the lagoon large patches of dense algal cover are found consisting of *Caulerpa*, *Hydroclathrus*, *Chaetomorpha* and *Cystoseira*. The presence of this dense algal cover is attributed to the greater water depth and circulation on this shore and also to the fact that nutrients would tend to be blown to the northern shore.

(*e*) *Zonation on mangroves*

On the trunks, leaves and branches of the mangrove trees *Littorina scabra* is common; it exhibits a strong polymorphism; individuals on leaves tend to be lighter in colour than those on tree trunks. There is also great variation in size of this species in various parts of the lagoon, to which the species is restricted. On the roots and trunks the barnacle *Tetrachthamalus oblitteratus* occurs with occasional byssate clusters of *Isognomon dentifer* and rarely the oyster *Crassostrea cucullata*. In some areas the algae *Bostrychia* and *Caloglossa* are abundant. Near channels the fauna at the base of the mangroves is quite diverse and the ophiuroid *Ophiocoma brevipes*, and the gastropods *Cypraea annulus* and *Nassarius reticulatus* occur amongst the roots and pneumatophores. The crabs *Helice leachii*, *Metopograpsus messor*, *Sesarma meinerti*, and *Cardisoma carnifex* may be present.

Along most of the lagoon shore the mangrove fringe is relatively narrow, and rocky headlands and islets are frequent. However, along the south coast it is penetrated by numerous creeks and embayments such as those at Bras Anse Dubois (26200, 04800) and Bras Takamaka (3410, 0700). Here in the creeks the mangrove fringe is wider but in the creek there may be accumulations of fine grey silt which is frequently flocculent.

These creeks show a characteristic zonation of organisms; lining the creeks are rocky cliff lines with a mangrove fringe on a rock substrate with only a thin sediment cover. For a few metres in front of the mangroves there is an undulating rock area with a fauna of *Uca tetragonon*, *Cerithium morum* and *Terebralia palustris* with blue-green algae on the rock surface. This passes into an area of accumulation of fine grey silt frequently with a blue-green algal crust which may show sun-cracked surface. This mud is inhabited primarily by the crab *Macropthalamus parvimanus* and polychaetes; the molluscs *Natica marochiensis* and *Quidnipagus palatam* may occur. In the centre of the creek there is frequently standing water on a mud or rock bottom. This may be occupied by *Cerithium morum* and the crab *Thalamita crenata*.

(*f*) *Land-enclosed marine pools*

At many sites on Aldabra there are land-locked tidal pools which support marine faunas and flora. These pools range in salinity from fairly normal marine to more or less fresh water (McKenzie, this volume, p. 261). They range in size up to about 100 m in length; they may be shallow and basin-like or with a rim of undercut cliff up to 2.5 m in height.

The pools were studied near Settlement on Ile Picard (05900, 09400), where there is a pool surrounded by an undercut cliff 2.5 m high and with a flat rock bottom; a long narrow pool at the east end of Middle Island (29700, 1180) with an undercut cliff and a mangrove fringe of *Rhizophora*; and a shallow basin-like pool filled with sediment at Anse Mais (06600, 0430).

In all these pools the molluscan fauna is very restricted and the only species commonly found are *Nerita undata*, *Planaxis sulcata*, *Cerithium morum*, *Siphonaria* sp., an unidentified buccinid and the chiton *Acanthopleura brevispinosa*.

In the Picard pool the eulittoral zone is occupied by *Acanthopleura*, *Nerita undata* and *Planaxis sulcatus*, and the bottom of the pool which is always water covered is colonized by large numbers of *Cerithium morum*. A small ophiuroid *Amphipholis squamata* and the muricid gastropod are also present on the bottom of the pools. In the Middle Island pool no *Littorina* or *Nerita* are found and the eulittoral zone on the rock is occupied by *Acanthopleura brevispinosa* and *Cerithium morum*; the latter ranges all over the bottom of the pool also. The eulittoral on the mangroves is colonized by *Planaxis sulcata*.

The algae of these pools are remarkable, for the Picard pool contains growths of *Valonia*, *Caulerpa*, *Ulva* and on the rocks *Bostrychia* and *Caloglossa*. The Middle Island pool has festoons of green algae hanging from the roof of the undercut; epilithic hemispheres of *Valonia* colonize the eulittoral on rock, and a finely branching red alga on mangrove roots. The floor of the pool is colonized by massive growths of *Caulerpa racemosa* and *Chaetomorpha*. Among these algae ophiuroids and a small holothurian occur.

The individuals of *Acanthopleura* found within these pools are substantially smaller than individuals from populations from the seaward side of the atoll. It is noticeable that the molluscan fauna is restricted and it is suggested that this paucity is because of dispersal problems. Very few of these pools have obvious direct contact with the open sea and because intertidal mollusca tend to have short or no pelagic larval lives (J. B. Lewis 1960) these species will tend to be excluded and only those with longer larva lives such as *Acanthopleura* will reach these pools.

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(*g*) *Sandy intertidal shores*

Sandy beaches are rare around the atoll, the only extensive beach being that at the western end of Ile Picard extending from north of the Settlement to just north of Passe Femme. Along much of this length the beach is fronted by a beach-rock exposure. Other beaches are very small and restricted in extent. They occur at such places as Anse Cèdres (3600, 11301), Anse Porche (14480, 12600), Anse Grande Poche (10180, 10400) and a series of beaches at the western end of South Island. The perched beaches along the exposed sites do not develop a marine fauna and are not considered here.

The macrofauna of the beaches is very limited. The most conspicuous element is the scavenging crab *Ocypode ceratopthalma* which makes its burrows at about the h.w.s. line. Higher on the beach on the berm and other sandy areas another species *O. cordimana* occurs.

Along the sections of the Picard beach where there is no beach-rock a burrowing suspension feeding bivalve *Atactodea glabrata* occurs in vast numbers. The only other sites where this bivalve was found were the beach at Grande Poche and the intertidal portion of a lagoon sand bank near Iles Chalen (0800, 7020). On the Picard beach a single valve only of *Donax faba* was found, this species is an abundant constituent of the sandy beach fauna in other islands in the western Indian Ocean.

4. Organisms of the intertidal area

(*a*) Littorina *species*

Two species of *Littorina* are common: *L. glabrata* occurs on rocky shores in the littoral fringe on both seaward and lagoon shores. *L. scabra* is confined to lagoon shores and is common on the roots and trunks of mangroves but rare on rock substrates. A third species, *L. granocostata*, was found at only two sites; East Channel (30730, 12330) and Dune d'Messe (19180, 01210). It is very inconspicuous and undoubtedly more common; it occupies a lower position in the littoral fringe than *L. glabrata*. Struhsaker (1966) found that in Hawaii *L. scabra* inhabits calm mangrove areas and is adapted for breeding in dry conditions. The eggs are brooded in the mantle cavity so that development can proceed even when conditions for spawning are unfavourable.

A small group of *Tectarius* sp. was found on the Picard beach-rock in September 1969 inhabiting the same crevices as *L. glabrata*.

(*b*) Nerita *species*

Five species of *Nerita* are common around the atoll (a sixth species *N. debilis* is rare) and they show interesting distribution patterns. With the exception of channel areas only one species, *N. undata*, commonly inhabits lagoon shores, although occasionally *N. albicilla* may be present. These and three other species are all found upon seaward shores; although they may be all present at the same shore they are separated by the position occupied upon the shore which appears to be related to their various abilities to withstand desiccation. Thus high on the shore in the littoral fringe the white thick shelled ribbed *N. plicata* occurs on both sheltered and exposed shores. On exposed shores the larger thicker shelled *N. textilis* is common (figure 21) occupying a slightly lower position than *N. plicata* and having a tendency to congregate around high pools. On sheltered shores *N. undata* occurs in the high eulittoral but usually in fairly sheltered sites; on exposed shores this species is larger and occupies more open sites. Low in the eulittoral and always in shaded and damp sites is *N. albicilla*, it usually remains in crevices and damp situations during the day. It is common on the more gently shelving shores of beach-rock and cobble spits and is more or less confined in distribution to sheltered shores. *N. polita* occurs on shores where there are small beaches at the base of the cliff and it spends a considerable portion of the daytime in the sand and appears to feed upon the rock substrate at night. This behaviour may be a protection against excessive desiccation although Fischer (1966*b*) has considered it a feeding phenomenon, *N. polita* being preadapted to the burrowing life.

N. textilis and to a lesser extent *N. plicata* show migratory movements up and down the cliff during the spring-neap tidal cycle. Daytime feeding in *N. textilis* occurs when the surrounded rock surface is dampened by wave splash but is suspended in heavy wave action.

No species of *Nerita* are found in the sublittoral zone. Fischer (1966*a*) has shown that species of *Nerita* can tolerate emersion for considerable periods of time. They cannot, however, survive prolonged immersion. The tolerance of emersion is approximately equivalent to their position on the shore. Thus of the species investigated by Fischer, *N. plicata* can survive up to 68 days in air, *N. undata* 11 to 36 days, *N. polita* 16 to 31 days and *N. albicilla* 6 to 21 days. This is in contrast to *Acanthopleura brevispinosa* and '*Purpura hippocostanum*' (*Thais aculeata*) which survived 4 and 2 days respectively. It has been shown by J. B. Lewis (1960) and Kolipinksi (in Fretter 1965) that four Floridan and Barbadian species of *Nerita* all copulate, have resistant egg capsules and free veligers with a long pelagic life.

During June to September 1969 copulations were observed in *N. plicata*, *N. textilis*, *N. undata* and *N. albicilla*. All these species lay egg capsules which in the three former species may be laid on open rock surfaces subject to severe insolation. The capsules of *N. albicilla*, however, are laid at the base of the eulittoral zone in damp and shaded sites beneath cobbles and overhangs.

(*c*) *Limpets*

Three species of patelliform gastropods occur in the eulittoral, with (figure 20) overlapping distributions. *Siphonaria madagascarensis* is a patelliform pulmonate and is the most widespread of the limpets occurring in the lagoon and on shores of all degrees of exposure. Purchon (1968) has observed a species of *Siphonaria* feeding only when emersed; when immersed the shell is tightly clamped to the rock, *Acmaea* cf. *profunda* occurs on all seaward shores high in the eulittoral where it occupies deeply cut circular depressions on the dissected limestone surface. The third species *Cellana cernica* occurs much lower on the shore in the mid-lower eulittoral, where it is much more abundant on exposed shores than sheltered shores.

(*d*) *Bivalves in the high intertidal*

A surprising occurrence in the intertidal fauna is the bivalve *Lasaea rubra*. This species occurs in Europe, West and South Africa, Azores, St Paul, Amsterdam Islands and Magellan Straits. In the Indian Ocean the species has been recorded from Madagascar (Dautzenberg 1929; Plante 1964), Rodriguez (Smith 1879 as *L. australis*) and other specimens in the British Museum (Natural History) collection originate from Natal and Praslin I. (Seychelles); both these latter collections were made among the byssus threads of *Isognomon dentifer*. On Aldabra it was found among the barnacle *Tetraclita squamosa*, in clumps of *Isognomon dentifer*, and in a land-locked tidal pool near Point Hodoul it was found in great abundance among the alga *Bostrychia*. However, it probably occurs at many more sites than found hitherto. Morton, Boney & Corner (1957) describe how this species is adapted to life in the high intertidal with conditions of brief submersion and hence short respiration and feeding times. It is an opportunistic species able to take fullest advantage of wave splash and experiments have shown its tolerance of prolonged conditions of high temperature and low humidity. Its small size is a distinct advantage in this respect.

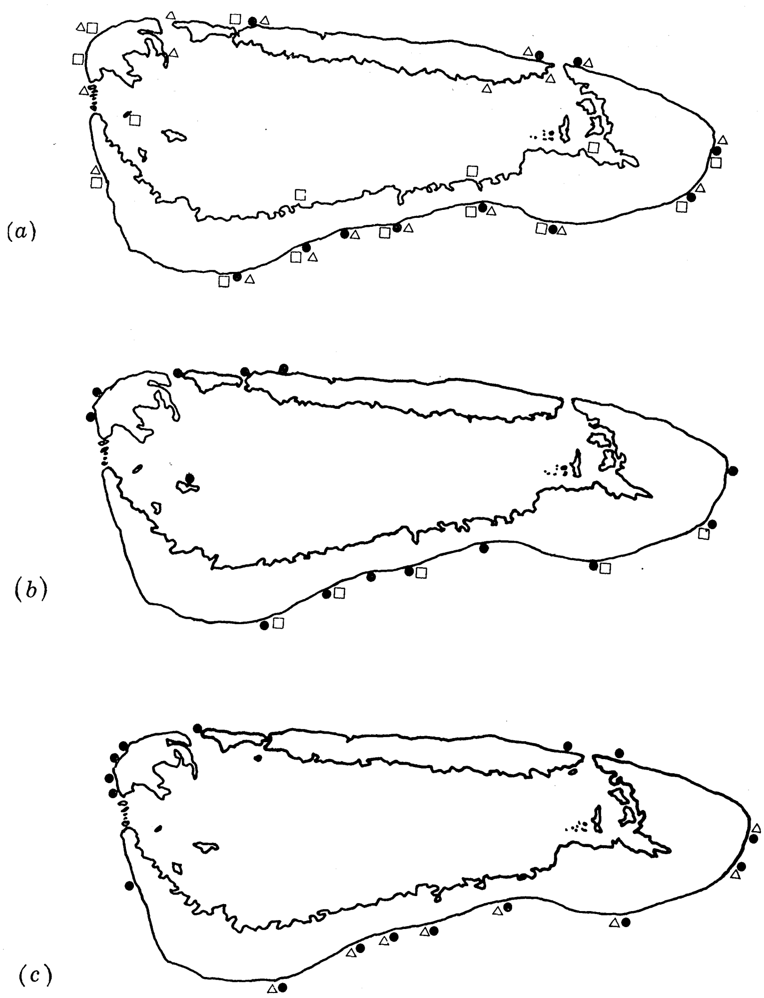

FIGURE 20. Recorded distribution of various intertidal mollusca around Aldabra: (*a*), □, *Siphonaria madagascarensis*; ●, *Cellana cernica*; △, *Acmaea* cf. *profunda*; (*b*), ●, *Conus chaldeus*; □, *C. ebraeus*; (*c*), ●, *Drupa morum*; △, *D. ricinus*.

Much has been written of the adaptations of *Lasaea rubra*, but more remarkable is another suspension feeding bivalve *Isognomon dentifer* which lives byssally attached high in the eulittoral and on exposed shores in the littoral fringe. It is much bigger than *Lasaea*, individuals have an average length of about 2 cm; the problems of life at high intertidal levels must be more intense for *Isognomon* than for *Lasaea*, for as Morton *et al.* (1957) has shown *Lasaea* is, because of its small size, capable of feeding in a very thin film of water. A similar film would not be supported over the irregular clumps of *Isognomon*. A detailed study of the biology and adaptations of this species would be rewarding. *Isognomon* lives in small byssate clumps either in hollows in the dissected rock or on the roof of the undercut on sheltered shores. It therefore lives in a position in which wave splash is at a maximum as well as being shaded. In the Seychelles where there is more cloud cover *I. dentifer* lives in open sites (Taylor 1968, plate 15).

The crevices between *Isognomon* individuals and among the byssus threads are the shelter for small gastropods such as *Fossarus lamellosus*, *Peasiella* sp., juvenile *Nerita* and *Lasaea rubra*.

(*e*) *Muricacea*

The most abundant of the gastropod predators of the intertidal are species of the superfamily Muricacea. Species of this superfamily are able to exist on steep rocky slopes from which species of *Conus* are apparently excluded. Thirteen species are commonly found, which vary in their abundance, relation to exposure, position on the shore, size and prey.

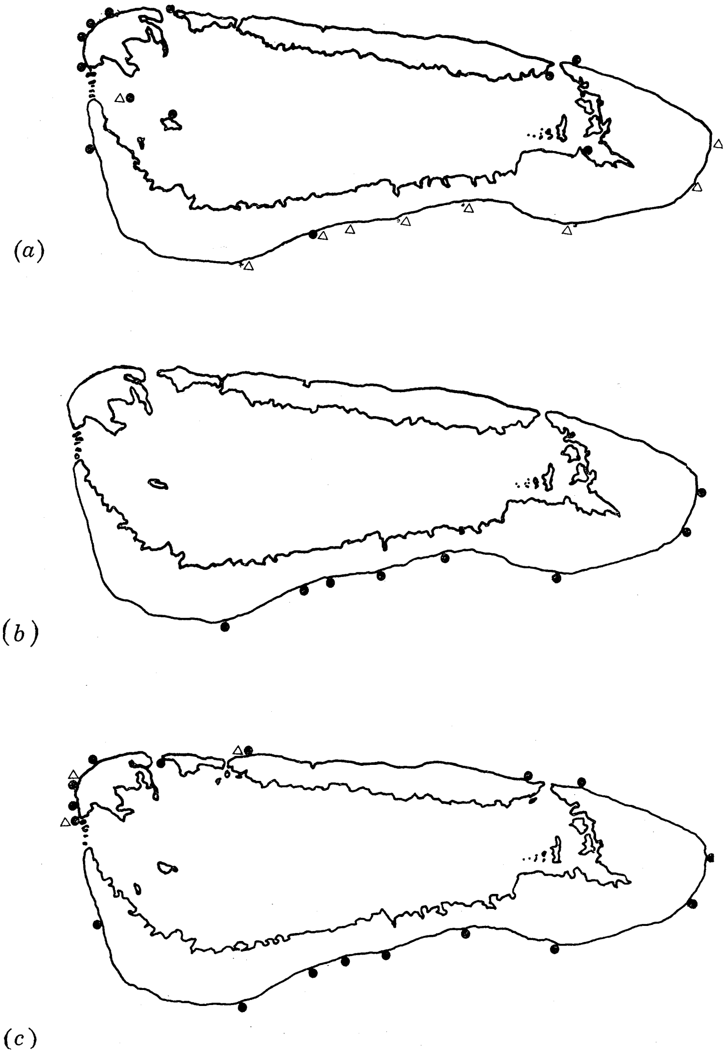

FIGURE 21. Recorded distribution of some intertidal Mollusca around Aldabra: (*a*), ●, *Nerita textilis*; △, *N. albicilla*; (*b*), *Purpura rudolphi*; (*c*), ●, *Morula granulata*; △, *M. anaxeres*.

Six species are commonly found in the eulittoral zone. *Morula granulata* occurs on all shores (figure 21) and is the most abundant predator. It occurs in the middle and lower parts of the eulittoral zone and was observed feeding upon tubiculous eunicid worms, *Brachiodontes* and *Tetrachthamalus*. The closely related species *Morula anaxeres* is much less common and was found only on the sheltered shores at the western end of the atoll (figure 21). It occupies a higher

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position on the shore than *M. granulata* and feeds upon *Tetrachthamalus* and sometimes *Nerita* eggs. Wu (1965) has shown that the morulid radula is adapted for boring and rasping. Another species common on sheltered shores is *Drupa marginatra* which lives in the upper eulittoral zone and feeds predominantly upon *Acmaea*, *Tetrachthamalus* and tubiculous eunicid worms. *Thais aculeata* occurs upon all shores but is much more common at exposed sites. It feeds mainly upon the limpets *Acmaea* and *Siphonaria*, but where these are sparse then upon *Tetrachthamalus* and *Lithotrya*. Restricted in distribution to the exposed shores of the south and east is *Purpura rudolphi* (figure 21). This species feeds predominantly upon the large barnacle *Tetraclita squamosa* but may also take *Acmaea* and *Siphonaria*. Two other species *Drupa fenestrata* and *Thais tuberosa* were found on exposed shores, the former was observed feeding upon *Nerita textilis* eggs.

Drupa ricinus occurs in the eulittoral of both sheltered and exposed shores (figure 20). On exposed shores such as Cinq Cases it occurs on open surfaces but at sheltered sites it is found in crevices and under boulders. It was observed feeding both upon sponges and the tubiculous eunicid worm which forms a crust in the eulittoral. Wu (1965) records that in Hawaii this species is not a driller but has a varied diet including carrion. The 'drupid' radula is adapted for rasping. A larger closely related species *Drupa morum* is found only at exposed sites (figure 20) but occurs on the boulder zone of the seaward platform at more sheltered sites. The high energy conditions of the boulder zone are presumably comparable to that of the cliff line on exposed shores.

In the low eulittoral and sublittoral fringe various other species such as *Morula uva*, *Nassa francolina*, *Drupa marginatra*, *D. margariticola* and *Maculotriton digitalis* occur, but these are not as individually abundant as the species of higher levels. Possibly the presence of predator species from other superfamilies such as the Cymatidae, Volutacea and Conacea is a competitive factor.

(*f*) *Species of* Conus

Two species of the gastropod genus *Conus* commonly occur in the mid to low eulittoral, these are *C. ebraeus* and *C. sponsalis*. Other species such as *C. coronatus*, *C. chaldeus*, *C. flavidus*, *C. lividus* and *C. rattus*, are common in the sublittoral fringe, being more abundant on exposed than on sheltered shores. Several other species are found in the sublittoral fringe but they are generally less common; 27 *Conus* species are found around the atoll.

Detailed observations on the feeding habits of this predatory genus have been made by Kohn (1959, 1960, 1966, 1968) and the usual diets of many species have been established. The species listed above commonly feed in varying proportions upon eunicid, nereid, maldanid and terebellid worms. On the beach-rock at Settlement on Ile Picard *C. ebraeus* feeds upon the coiled tubiculous eunicid which encrusts the rock surface in the low eulittoral zone.

Each species of *Conus* shows certain habitat associations (Kohn 1968) and work is in progress on an analysis of several thousand microhabitat collection records of various gastropod families including *Conus* around Aldabra. An example of specific differences may be seen by comparing the range of two closely related species *C. chaldeus* and *C. ebraeus* (figure 20). Whereas *C. ebraeus* occurs on both sheltered and exposed shores in the eulittoral and sublittoral fringe zones. *C. chaldeus* has been found in the sublittoral fringe of exposed shores only.

A limiting factor on the distribution of *Conus* in the intertidal around Aldabra may be the shore topography. *Conus* species are absent from the eulittoral zones of shores with vertical or steep profiles, but are common on the shallowly dipping beach-rock or at the base of ramp cliffs. Among the carnivorous Mollusca only the Muricacea seem able to live successfully upon steeply sloping surfaces. The increase of diversity of *Conus* species on the lower shore may be attributable to an increase in the diversity of prey species. For instance *C. catus*, a piscivorous species, is naturally confined to sublittoral sites.

(*g*) Acanthopleura brevispinosa

This chiton is the most conspicuous of the algal grazers; it is common on all shores from very exposed to very sheltered including all sites in the lagoon. Individuals in the lagoon are smaller than those on seaward sites, but are larger than individuals found in land-enclosed tidal pools.

(*h*) *Barnacles*

The most abundant barnacle is the only known species of the recently described, small, four-plated chthalamid genus *Tetrachthamalus oblitteratus* (Newman 1967). This barnacle has been reported as occurring in the Red Sea, Seychelles, Mauritius and Aldabra.

On the shores of Aldabra *Tetrachthamalus* occurs high on the shore and the first appearance in abundance is taken as the top of the eulittoral zone. On sheltered shores it extends in a belt about 1 m wide, but on exposed shores this is extended to 2.5 m. It occurs on shores of varying exposure, although the distribution in the lagoon is largely confined to the vicinity of channels; this last fact may be a dispersion phenomenon. It is commonly found on mangroves roots and pneumatophores. Southward (1967) has shown by experiments on cirral activity, heat coma and behaviour that the species is well adapted for life on a tropical shore and he suggests that four-platedness may be an adaptation to resist desiccation. However, observed densities of *Tetrachthamalus* are very low compared with barnacles of temperate areas and at many sites the species must be actively searched for. There is no competition for space with any other organism and substrate may be a limiting factor, for in the Seychelles on granite substrates densities are generally higher (Taylor 1968, plate 15, figure 26). However, in the Seychelles cloud cover is higher than in Aldabra and insolation and desiccation effects are consequently less.

The only other common intertidal encrusting barnacle is *Tetraclita squamosa rufotincta* found lower on the shore beneath the most abundant occurrence of *Tetrachthamalus*. It is usually only locally common, occurring in small groups rather than occupying a continuous belt. It is found on most seaward sites and in the channels but it is generally more abuhdant on exposed shores being common at Entrebois, Dune Jean-Louis, and Cinq Cases. It is absent from the lagoon.

A third species *Tetraclita wireni africana* was found only once on the cliffs at Dune Jean-Louis where it encrusted the shells of the gastropod *Drupa ricinus* low in the eulittoral; otherwise this species occurs on the boulders at the seaward edge of the seaward platform.

Two more species of barnacle were found in September 1969, these await identification.

A boring pedunculate barnacle *Lithotrya* sp., found in the eulittoral at many sites, is discussed below.

(*i*) *Crabs*

The fast-moving grapsid crab *Grapsus tenuicrustatus* is a most conspicuous member of the intertidal, occurring in vast numbers on some shores. At low water it ranges throughout the intertidal zone but at high water it is restricted to the littoral fringe. It feeds upon algae, lichen and organic debris. Another species *G. fourmanoiri* was found in high pools on exposed shores. *Geograpsus stormi*, a species normally associated with the supralittoral, was sometimes seen in the littoral fringe of damp shady sites.

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Common on the beach-rock and at south coast sites is the large xanthid *Eriphia laevimana* it is confined to the eulittoral and is active at low-water feeding upon smaller crabs and molluscs. Another crab of the high eulittoral is *Euruppellia annulipes* which inhabits crevices and was observed feeding upon juvenile *Acanthopleura brevispinosa*.

In the low eulittoral and sublittoral fringe a wide variety of crabs is found. They are mostly cryptofaunal species remaining hidden beneath crevices and beneath blocks during low water during the day. These species include *Percnon planissimum*, *Epixanthus frontalis*, *Xanthias lamarcki*, *Pilumnus longicornis*, *Leptodius quinquedentatus* and *Dromidiopsis dormia*. Other common Crustacea are large numbers of hermit crabs *Calcinus* sp., *Petrolisthes lamarcki* and stomatopods.

5. Discussion

(*a*) *Biological exposure scale*

A biologically defined exposure scale such as that developed by Ballantine (1961) may be tentatively proposed for Aldabra. The changes in zonation from sheltered to exposed conditions are completely transitional but they may usefully be divided for descriptive and comparative purposes into arbitary types. The main characteristics of each of the exposure categories recognized are listed below and shown graphically in figure 22.

(i) *Very sheltered shores*

This type is commonly found within the lagoon, cliffs are low with severe undercutting, the base of the undercut commonly emersed at low water. May be represented by mangrove trunks and roots.

(*a*) The littoral fringe is narrow with *Littorina glabrata*, some *Isognomon dentifer*, *L. scabra* on mangroves.

(*b*) Blue-green algae and *Bostrychia*/*Caloglossa* the only algae present in the high eulittoral, *Enteromorpha* and *Colpomenia* may occur lower down.

(*c*) *Tetrachthamalus* sparse, *Siphonaria* and *Acanthopleura* sporadic. *Nerita undata* the only common neritid.

(*d*) Muricid and conid predatory gastropods absent.

(*e*) *Cerithium morum* abundant in the low eulittoral, with byssate masses of *Brachiodontes variabilis* in some places.

(ii) *Sheltered shores*

This category includes cliffs at the western end of the atoll and the north shore of Middle Island. The cliffs are higher, about 3 m, and undercut to a greater or lesser extent, this category also includes the Picard beach-rock.

(*a*) Littoral fringe with *Littorina glabrata* and *Nerita plicata* common.

(*b*) *Tetrachthamalus*, *Siphonaria*, *Acmaea*, *Acanthopleura* and *Nerita undata* characterize the high eulittoral.

(*c*) In the low eulittoral the algae *Enteromorpha*, *Ulva* and *Ceramium* occur as well as a pink encrusting ascidian, and tubiculous eunicid worms.

(*d*) *Morula granulata*, *Engina mendicaria*, *Lithophaga nasuta* and *Brachiodontes variabliis* are typical molluscs of this level.

(*e*) The sublittoral fringe is marked by algae such as *Codium*, *Laurencia*, *Peyssonelia* and *Dictyurus*, and a little lower the marine phanerogams *Thalassia* and *Cymodocea*.

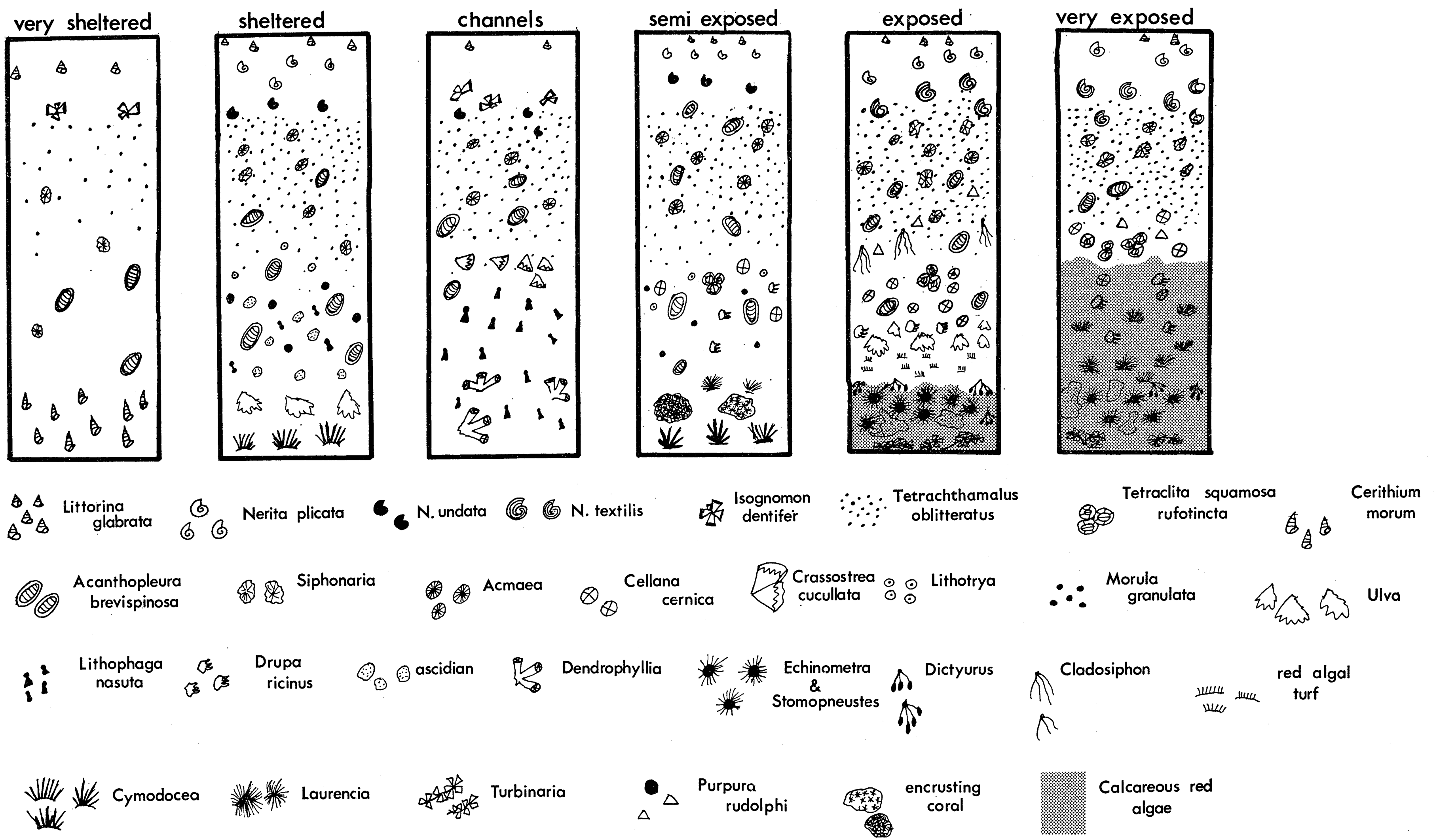

FIGURE 22. Diagrammatic representation of the major features of intertidal zonation patterns at various degrees of exposure around Aldabra. The eulittoral is reduced to the same scale in each case for comparative purposes.

(iii) *Semi-exposed shores*

Cliffs on these shores are vertical or slope steeply landwards, at the base there is a moat. Cliffs of this type are seen at the northeast shore of Middle Island or the southwest of South Island. The cliffs are about 5 m high.

(*a*) The littoral fringe is marked by *Littorina glabrata* and *Nerita plicata*. Above the barnacle line is *N. undata*.

(*b*) The eulittoral marked by the appearance of common *Tetrachthamalus*, *Acanthopleura*, *Acmaea* and *Lithotrya*.

(*c*) In the low eulittoral *Morula granulata*, *Drupa ricinus* and *Onchidium* are the common mollusca.

(*d*) The sublittoral fringe is occupied by corals and algae such as *Laurencia* and *Halimeda*, and lower in the sublittoral *Cymodocea*.

(iv) *Exposed shores*

Cliffs of these shores are ramp-like with some eulittoral pools and a flat top. Shores of this type are found from Point au Vaqua to Takamaka au bord de la Mer.

(*a*) The littoral fringe is very wide with *Littorina glabrata* at the extreme landward portion and *Nerita plicata* and *N. textilis* in succession at the seaward edge.

(*b*) *Tetrachthamalus* abundant, *Acanthopleura*, *Acmaea* and *Siphonaria* at the top of the eulittoral.

(*c*) The mid-eulittoral is characterized by *Tetraclita squamosa rufotincta*, *Cellana cernica*, *Purpura rudolphi*, *Morula granulata* and *Cladosiphon* in pools.

(*d*) The eulittoral has distinct belts of *Ulva* and *Ceramium*.

(*e*) The sublittoral fringe is characterized by the algae *Dictyurus*, *Botryocladia*, *Gelidium*, pads of colonial ascidians, and the echinoids *Stomopneustes* and *Echinometra*. There is great diversity of mollusca, especially species of *Turbo*, *Trochus*, *Conus* and *Cypraea caputserpentis* and *C. mauritiana*. Most of the sublittoral platform is clothed in the algae *Turbinaria* and *Sargassum*, and locally *Cymodocea* and *Thalassia*.

(v) *Very exposed shores*

These are found at the extreme easterly end of the atoll; the cliffs are ramp-like with a step formed by a platform at the mid-eulittoral level.

(*a*) Organisms of the littoral fringe and high eulittoral are essentially similar to those of exposed shores.

(*b*) In the low eulittoral the platform is coated with a crust of red calcareous algae and cushion growths of *Laurencia*; tubiculous eunicids, *Drupa ricinus* and *Morula granulata* are common.

(*c*) Echinoid zone similar to exposed shores in the sublittoral fringe except that *Laurencia* abundant. The sublittoral is characterized by *Turbinaria* and calcareous red algae.

(*b*) *Diversity and abundance*

The general observation that in the littoral fringe and eulittoral zones species diversity is low and population density high, but in the sublittoral fringe species diversity is high and population density low, is true for the intertidal rocky shores of Aldabra.

The higher diversity lower on the shore has been explained by reference to various factors such as increased habitat complexity (Kohn 1968) and predation intensity (Paine 1966). Paine put forward the hypothesis that 'local species diversity is directly related to the efficiency with which predators prevent the monopolization of the major environmental requisites by one species'. However, when consideration of the increased diversity from the intertidal to the sublittoral fringe is made it must be borne in mind that the species of the eulittoral and littoral fringe must be tolerant of emersion to a greater or lesser extent. This limiting factor would account for the reduced diversity higher on the shore, allowing the wider exploitation of the habitat by fewer species resulting in greater population density. Sanders (1968) distinguishes between physically controlled and biologically accommodated communities. Thus the organisms of the intertidal rocky shore are predominantly physically regulated communities and adaptations are primarily to the physical environment, and biological interactions are poorly developed. Where conditions are more uniform as in the shallow sublittoral zone the communities are developed by processes of biological interactions resulting in a great diversity of species.

In the littoral fringe and high eulittoral predators, except for birds, are infrequent and the fauna is dominated by algal-grazing and suspension-feeding species. Predators such as the gastropods Muricacea and Conacea are able only to inhabit the low and mid-eulittoral. Therefore any predation effect as suggested by Paine (1966) is operative only at these levels. Although predation intensity has increased, so has habitat complexity and also animals living at lower levels do not suffer such prolonged periods of emersion. Increased diversity down the shore should therefore be considered as a complex interaction of many factors including varying predation intensity, increased habitat diversity, less emersion, and the gradient from a physically controlled community to a biologically regulated one.

Table 1 shows the number of mollusc species recorded at successive levels down the shore on a transect at Dune d'Messe. There is a massive increase in diversity in the sublittoral fringe and upper sublittoral zones. A similar increase is seen in other phyla. Not only is there a substantial change in diversity but there is an abrupt change in composition of the fauna at the bottom of the eulittoral zone. None of the molluscan species represented in the eulittoral zone is found in the shallow sublittoral area. This situation is possibly more accentuated on the shores of Aldabra because of the sharp change in substrate topography at the base of the eulittoral zone from cliff to platform. Thus at Dune d'Messe there is a sharp separation of species tolerant of emersion with adaptations for intertidal life and the species of the sublittoral fringe which are infrequently emersed. More gently sloping shores show a narrow transition zone at the base of the sublittoral zone.

If a crude analysis of feeding types in the molluscan fauna is made and expressed as a percentage of the total molluscan fauna (table 1) it is seen that higher on the shore algal grazers

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Description of plate 15

Figure 23. 1, *Trochus flammulatus* (Gould); 2, *Tectus mauritianus* Lamarck; 3, *Cellana cernica* (H. Adams); 4, *Siphonaria madagascarensis* Ohdner; 5, *Acmaea* cf. *profunda* (Deshayes); 6, *Nerita albicilla* Linnaeus; 7, *N. plicata* Linnaeus; 8, *N. textilis* Dillwyn; 9, *N. undata* Linnaeus; 10, *Planaxis sulcatus* (Born); 11, *Nerita polita* Linnaeus; 12, *Littorina glabrata* Philippi; 13. *Littorina* cf. *granocostata* Reeve; 14, *L. scabra* Linnaeus; 15, *Cerithium morum* Lamarck; 16, *Vasum turbinellus* (Linnaeus); 17, *Purpura rudolphi* (Lamarck); 18, *Drupa morum* Röding; 19, *D. ricinus* (Linnaeus); 20, *Terebralia palustris* (Linnaeus); 21, *Thais aculeata* Deshayes; 22, *Morula granulata* (Duclos); 23, *M. anaxeres* (Duclos); 24, *M. uva* Röding; 25, *Cypraea caputserpentis* Linnaeus; 26, *Brachiodontes variabilis* (Krauss); 27, *Isognomon dentifer* (Krauss); 28, *Acanthopleura brevispinosa* (Sowerby); 29, *Conus ebraeus* Linnaeus; 30, *Crassostrea cucullata* (Born).

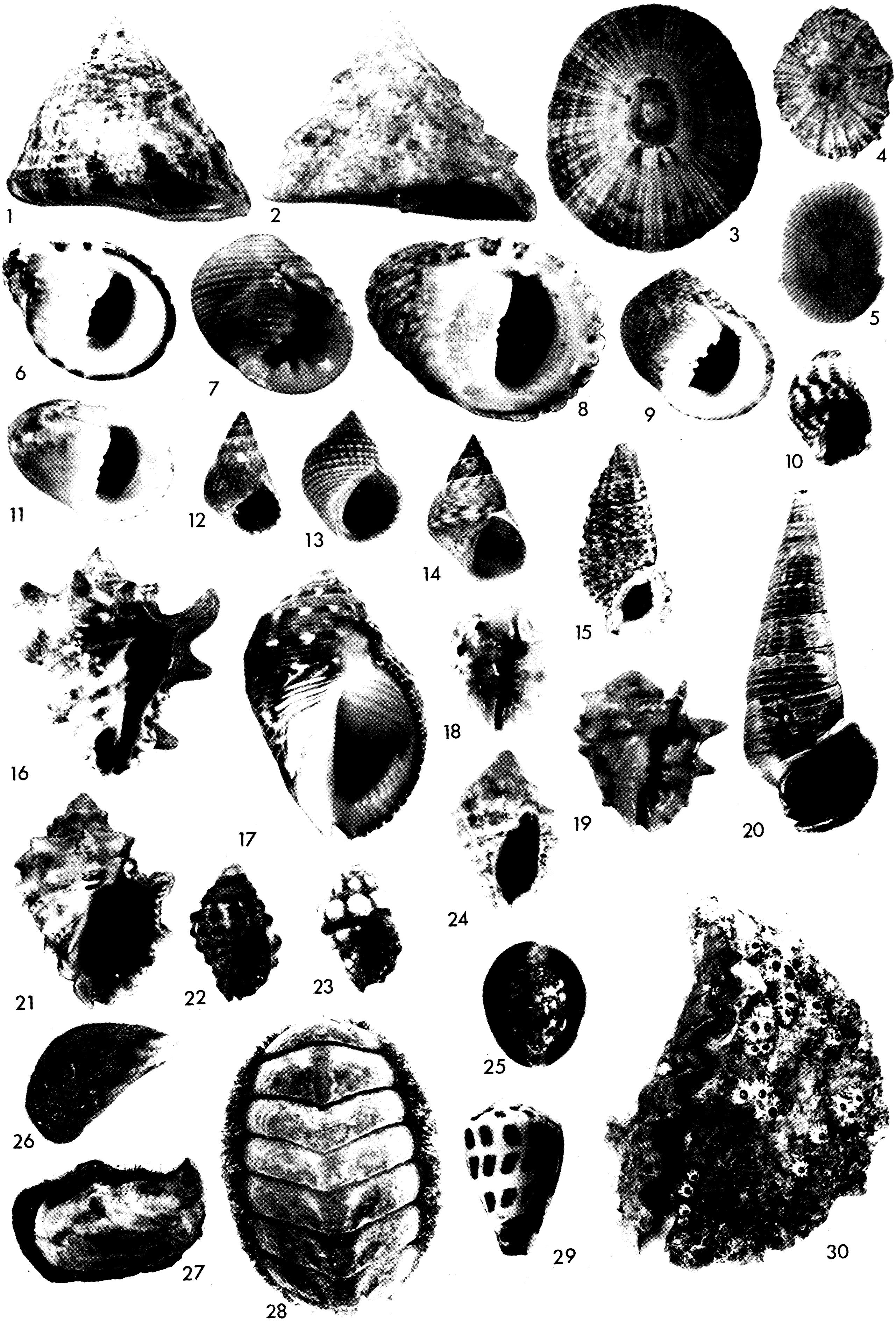

Figure 23. For legend see facing page.

(Facing p. 206)

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are prevalent, but disappear in the lower eulittoral zone and are replaced in the sublittoral by a different set of grazing species. The molluscan fauna of the lower eulittoral zone is dominated by predators which are absent from the higher sites. Many predator species are present in the sublittoral fringe but these are again different species from those of the eulittoral zone. Similar trends down the shore can be seen in the rest of the fauna. However, the number of suspension-feeders is higher (barnacles, etc.) and remains fairly constant down the shore. The rock-boring polychaetes lower on the shore were not adequately sampled, but they must be the major food source of many predators in the low eulittoral.

Table 1. Number of mollusc species on the shore at a transect at Dune d'Messe and the percentage composition of various feeding types

ht above e.l.w.s. m	total mollusc species	% algal grazers	% suspension-feeders	% predators
6	1	100	—	—
5	2	50	50	—
4	3	100	—	—
3	6	66	—	33
2	6	50	—	50
1	3	—	—	100
0	37	24	24	52

It is remarkable how few families of gastropods are present in the littoral fringe and eulittoral zones compared with the diversity found in the shallow sublittoral. Species found in the eulittoral zone are rarely found in the sublittoral. It seems that once emersion is tolerated separation from the sublittoral becomes more or less complete, although it is conceivable that some families have never occurred in the sublittoral. In the Conacea only a few out of many species, notably *C. ebraeus* and *C. sponsalis* occur in the eulittoral zone. Are these species the only species tolerant of emersion or is their distribution controlled by the distribution of prey species? Food specialization by species of Muricacea may have narrowed their vertical range. The more species of predators able to tolerate emersion, the more will habitat subdivision and food specialization occur narrowing the range of individual species and thus increasing the separation from the sublittoral. J. B. Lewis (1960) has shown how this separation of littoral forms from the sublittoral has been partially caused by reproductive isolation; he showed that in Barbados 67 % of intertidal species were copulators, the rest having external fertilization. Further, 60 % of the species produced egg capsules or had very short larval lives, the remaining species inhabited the low eulittoral or were barnacles and worms. He concluded that reproduction and larval history adaptations in the species studied limited dispersal so that settlement in the narrow intertidal is more certain. The adults tend to be copulators, to be oviparous or to produce egg capsules, and the larvae tend to have a much shortened free larval life.

On lagoon shores the intertidal fauna is sparse and shows very little diversity. This may be attributed to the peculiar conditions found within the lagoon. In the central areas circulation is not good and the waters are very tubid; it seems that the lagoon water merely moves back and forth with the tides. Exchange of water with the open sea takes place only in the channel areas where the fauna and flora is correspondingly more abundant and diverse. The lack of circulation means that movement of food, carbon dioxide, etc., is poor but also that larvae of intertidal animals will not easily reach the central lagoon area, thus contributing to the lack of diversity.

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Densities of animals in the eulittoral zone of Aldabra are low when compared with temperate areas. Indeed if the abundance notation system developed by Crisp & Southward (1958) for temperate shores is used on Aldabra then all the observed densities fall into their lower abundance categories. However Spight (1967) has indicated that population density gives a poor estimate of both biomass production and of competition. The demand for resources, which is a determinant of competition, is directly proportional to biomass production rate and not proportional to population density.

One of the most notable features of the intertidal of the atoll when compared with temperate shores is the lack of abundant macroscopic algae, particularly the brown algae. Large brown algae such as *Sargassum* and *Turbinaria* are however common in the sublittoral fringe and in the sublittoral. Their absence from the eulittoral is probably because of an inability to tolerate emersion under the high insolation and desiccation conditions experienced upon these shores. The number of brown algae species is also significantly lower in the tropics (J. H. Price, personal communication). The only common macroscopic algae occurring in the eulittoral are *Enteromorpha* and *Ulva*, these form distinct belts in the eulittoral on the beach-rock at Settlement on Ile Picard (05560, 10080). *Ulva* forms a belt low in the eulittoral on exposed shores, a rather low situation of *Ulva*. *Cladosiphon* occupies pools in the eulittoral on exposed shores and appears able to tolerate the extreme conditions experienced in these pools but not emersion. On very exposed shores with constant wave action and only limited drying in the low eulittoral a crust of calcareous red algae *Lithophyllum* and *Porolithon* is formed. These forms are notoriously intolerant of desiccation and are only present at these levels on very exposed shores or under constant immersion in pools. Much of the littoral fringe and eulittoral zones are covered by endo- and epilithic blue-green algae. Although not conspicuous they are ubiquitous on Aldabra shores.

This absence of macroscopic algae is thought to be due to excessive desiccation effects experienced in the eulittoral. It is possible that newly settled sporelings may be removed efficiently by grazing animals. Another point of view might be that Aldabra shores represent an early or arrested stage in succession. It has been shown that, upon fouling plates or cleared shores, both *Enteromorpha* and *Ulva* are dominant in the early stages of succession (Smith 1968). It could be that on Aldabra later stages of succession are suppressed and the community stabilized at the *Enteromorpha–Ulva* stage.

The lack of macroscopic algae does not necessarily mean that the primary productivity of the shore is reduced. The sites occupied by brown algae in temperate areas are occupied by smaller blue-green and green species which are more tolerant of the conditions. The production rate is continuous throughout the year. Where large algal masses are present on the shore only the sporelings and small species are usually accessible to grazing animals so therefore small epilithic algae may represent a more efficient energy transfer to primary consumers. Paine (1966) has suggested that an increased stability of primary productivity may lead to an increased capacity of the system to support higher level consumers.

(*c*) *Cliff erosion by intertidal organisms*

Although much of the erosion of the cliffs around Aldabra is undoubtedly solutional significant contribution must be made by the activities of intertidal organisms. This erosion may involve the active removal of material from the cliff or a weakening of the structure facilitating mechanical breakdown.

(i) *Grazing*

The grazing activity of intertidal Mollusca upon epilithic algae and sporelings is probably the most important organic agent in limestone erosion in the intertidal. Mollusca such as species of *Littorina*, *Nerita*, the limpets, the chiton *Acanthopleura* and the crab *Grapsus* contribute to this process. The molluscs feed by rasping of the radula (in chitons and some limpets this is made of magnetite or goethite, Towe & Lowenstam 1967); this rasping is accompanied by side-to-side movements of the head. In this way the molluscs scrape at the epilithic algae on the rock surface, but in the process much of the substrate itself is ingested or loosened by detachments of the algal filaments. Ingested sediment particles are expelled in the faeces and dispersed. Rates of erosion by *Littorina* have been investigated in California by North (1954). *Grapsus tenuicrustatus* feeds by tearing and scraping algae from the rock surface with its spoon-shaped chelae.

(ii) *Boring*

Various organisms such as bivalves, limpets, pedunculate barnacles, echinoids, sponges, sipunculid and polychaete worms are able to bore by mechanical or chemical means into the substrate. The role of these various organisms in the destruction of coral limestone has been discussed by Otter (1937). In the intertidal of Aldabra the most important of these species are *Lithotrya*, *Lithophaga*, *Echinometra*, *Stomopneustes*, sipunculid and polychaete worms and boring clionid sponges.

The burrows excavated by echinoids are hemispherical in shape and formed by mechanical action of the teeth and spines. The boring echinoids *Stomopneustes variolaris* and *Echinometra matthaei* are found in the intertidal only on the exposed and very exposed sites where they occupy, and are undoubtedly responsible for the formation of the notch at the base of the eulittoral on these shores.

The limpet *Acmaea profunda* inhabits deep (up to 1.5 cm) cylindrical depressions which it has excavated by shell movements and is responsible for a great deal of the microdissection seen on sheltered shores in the high eulittoral zone.

The borings by *Lithotrya* and *Lithophaga nasuta* are found at most seaward sites except the most exposed, and both are absent from the lagoon except in channel areas. *Lithotrya* is found in a belt about 50 cm wide at the top of the eulittoral zone, whereas *Lithophaga nasuta* appears in the low eulittoral and ranges down into the sublittoral zone. The siphons of *Lithophaga* secrete a lining to the borehole which is more resistant to solution than the surrounding rock, for these linings may be seen upstanding above the rock surface. However, in the long term the riddling of the base of the cliff probably weakens the structure facilitating mechanical erosion. In the mid and low eulittoral zones borings by sipunculid and polychaete worms are common; because of sampling problems their role is difficult to evaluate but on beach-rock exposures they are certainly abundant. Boring clionid sponges are important erosive agents in the low eulittoral zone at all seaward and channel sites around the atoll.

It is noteworthy that, although most of the rock borers are absent from lagoon shores, the degree of undercutting observed is generally greater than where they occur. However, the amount of mechanical activity of waves on seaward shores is greater so that deep undercut notches are unlikely to survive. The deepest incision of the notch is usually situated at m.h.w. mark where the density of intertidal organisms is low.

The filaments of blue-green and green algae penetrate the outer few millimetres of the limestone surface forming a dense network seen on broken surfaces as a green band. This algal layer is almost continuous on the rock surface of the littoral fringe and eulittoral zones. Small fragments of the rock surface may be flaked off by the activities of these algae (Revelle & Fairbridge 1957). Other algae in the intertidal zone may live closely adherent to the substrate and the holdfast filaments penetrate the interspaces between the sediment grains of the limestone.

Opposed to the erosive activity are the protective properties of certain organisms. Thus encrusting calcareous organisms such as barnacles, oysters, eunicid and serpulid worms, and calcareous algae protect the limestone surface from erosion and the activities of grazers and borers.

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Partial list of animals of the intertidal of Aldabra

Littoral fringe

Mollusca
- *Tectarius* sp.
- *Littorina glabrata* Philippi
- *Littorina* cf. *granocostata* Reeve
- *L. scabra* Linnaeus
- *Nerita plicata* Linnaeus
- *N. textilis* Dillwyn
- *Isognomon dentifer* (Krauss)

Crustacea
- *Geograpsus stormi* (de Man)
- *Grapsus tenuicrustatus* (Herbst)
- *G. fourmanoiri* Crosnier

Eulittoral

Mollusca:
- *Cellana cernica* (H. Adams)
- *Acmaea* cf. *profunda* (Deshayes)
- *Nerita albicilla* Linnaeus
- *N. plicata* Linnaeus
- *N. polita* Linnaeus
- *N. debilis* Dufo
- *N. textilis* Dillwyn
- *N. undata* Linnaeus
- *Cerithium morum* Lamarck
- *Fossarus lamellosus* Montrouzier
- *Terebralia palustris* (Linnaeus)
- *Planaxis sulcatus* (Born)
- *Engina mendicaria* (Linnaeus)
- *Purpura rudolphi* (Lamarck)
- *Thais aculeata* Deshayes
- *T. tuberosa* Röding
- *Morula anaxeres* (Duclos)
- *M. granulata* (Duclos)
- *M. uva* Röding
- *Drupa lobata* (Blainville)
- *D. margariticola* (Broderip)
- *D. marginatra* (Blainville)
- *D. morum* Röding
- *D. ricinus* (Linnaeus)
- *Vasum turbinellus* (Linnaeus)
- *Mitra cucumerina* Lamarck
- *Strigatella paupercula* (Linnaeus)
- *S. litterata* (Lamarck)
- *Conus sponsalis* Hwass
- *C. ebraeus* Linnaeus
- *Siphonaria madagascarensis* Ohdner
- *Onchidium* spp. (two species)
- *Barbatia decussata* (Sowerby)
- *Brachiodontes variabilis* Krauss
- *Lithophaga nasuta* Philippi
- *L. malaccana* Reeve
- *Crassostrea cucullata* (Born)
- *Chama* sp.
- *Lasaea rubra* Montagu
- *Atactodea glabrata* (Gmelin)
- *Acanthopleura brevispinosa* (Sowerby)

Crustacea: Cirrepdia
- *Lithotrya* sp.
- *Tetrachthamalus oblitteratus* Newman
- *Tetraclita squamosa rufotincta* Pilsbry
- *T. wireni africana* Nilsson-Cantell
- *Tetraclita* sp.

Decapoda
- *Grapsus tenuicrustatus* (Herbst)
- *Uca lactea* de Haan
- *U. tetragonon* (Herbst)
- *Helice leachii* Hess
- *Sesarma meinerti* de Man
- *Macropthalamus parvimanus* (Guerin)
- *Ocypode ceratopthalma* (Pallas)
- *O. cordimana* Desmarest
- *Metopograpsus messor* (Forskål)
- *M. thukuhar* (Owen)

Decapoda (*cont.*)
- *Epixanthus frontalis* (Milne Edwards)
- *Leptodius quinquedentatus* (Krauss)
- *Xanthias lamarcki* (Milne Edwards)
- *Actaea tomentosa* (Milne Edwards)
- *Dromidiopsis dormia* (Linnaeus)
- *Eriphia laevimana* (Guerin)
- *Euruppellia annulipes*
- *Pilumnus longicornis* (Hildago)
- *Calcinus laevimanus* (Randall)
- *Petrolisthes lamarcki* (Leach)

Sublittoral fringe and shallow sublittoral

There is a great diversity of species at these levels and only some of the more commonly occurring species are listed here. It is hoped that eventually a complete marine fauna for Aldabra will be compiled.

Mollusca
- *Turbo argyrostomus* Linnaeus
- *T. marmoratus* Linnaeus
- *Tectus mauritianus* (Gould)
- *Trochus flammulatus* Lamarck
- *Phasianella aethiopica* Philippi
- *Rhinoclavis sinensis* (Gmelin)
- *Cerithium nassoides* Sowerby
- *Vanikoro ligata* Recluz
- *Cypraea annulus* Linnaeus
- *C. arabica* Linnaeus
- *C. caputserpentis* Linnaeus
- *C. helvola* Linnaeus
- *C. histrio* Gmelin
- *C. kieneri* Hildago
- *C. mauritiana* Linnaeus
- *Columbella pardolina* Lamarck
- *Peristernia nassatula* (Lamarck)
- *Leucozonia smaragdula* (Linnaeus)
- *Cantharus undosus* (Linnaeus)
- *Columbella varians* Sowerby
- *Engina mendicaria* (Linnaens)
- *Nassarius gaudiosus* Hinds
- *Maculotriton digitalis* (A. Adams)
- *Nassa francolina* Bruguiere
- *Bursa granularis* (Röding)
- *B. rubeta* (Linnaeus)
- *Cypraecassis rufa* (Linnaeus)
- *Cymatium nicobaricum* (Röding)
- *Conus catus* Hwass
- *C. chaldeus* (Röding)
- *C. coronatus* Gmelin
- *C. ebraeus* Linnaeus
- *C. flavidus* Lamarck
- *C. lividus* Hwass
- *C. musicus* Hwass
- *C. rattus* Hwass
- *C. sponsalis* Hwass
- *Barbatia decussata* (Sowerby)
- *Arcopsis symmetrica* (Reeve)
- *Acar plicata* (Dillwyn)
- *Septifer bilocularis* (Linnaeus)
- *Modiolus auriculatus* (Krauss)
- *Isognomon perna* (Linnaeus)
- *I. legumen* (Gmelin)
- *Ostrea numisma* Lamarck
- *Chama aspersa* Reeve
- *Cardita variegata* (Bruguiere)

Echinoderms
- *Stomopneustes variolaris* (Lamarck)
- *Tripneustes gratilla* (Linnaeus)
- *Echinometra matthaei* (Linnaeus)
- *Heterocentrotus trigonarius* (Lamarck)
- *Echinoneus cyclostomus* Leske
- *Ophiocoma brevipes* Peters
- *O. erinaceus* Muller & Troschel
- *O. scolopendrina* (Lamarck)
- *O. valenciae* Muller & Troschel
- *Linckia multifora* (Lamarck)
- *Holothuria* (*Thymiosycia*) *hilla* (Lesson)
- *H.* (*Thymiosycia*) *impatiens* (Forskål)
- *H.* (*Thymiosycia*) *arenicola* Semper
- *H.* (*Semperothuria*) *cinerascens* Brandt
- *H.* (*Lessonothuria*) *pardalis* Selenka
- *Afrocucumis africana* (Semper)

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FIGURE 23. For legend see facing page.

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