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Hydroid, Amphineuran and Gastropod Zonation in the Littoral of the Caribbean Sea, Colombia.

With 48 Text-Figures.

KLAUS BANDEL & EBERHARD WEDLER.

Abstract.

[BANDEL, K. & WEDLER, E. (1987): Hydroid, Amphineuran and Gastropod Zonation in the Littoral of the Caribbean Sea, Colombia. — Senckenbergiana marit., **19** (1/2): 1-129, 48 figs.; Frankfurt a. M.]

Gastropods, amphineurans and hydroids of the Caribbean coast of Colombia near Santa Marta are characterized and placed into their specific environment. Some species are good indicators of supra-, eu-, and sublittoral zones, others reflect current conditions in occurrence and shape, others again are characteristic of larger or smaller ecologic units like a reef lagoon (large) or a tree trunk (small). A large group of species cannot be used for zone determination.

Hydroids as sessile coelenterates have to compete for space with other encrusting organisms and strongly reflect substrate, depth, light and water energy in shape and species composition.

Gastropods and amphineurans, mostly vagile molluscs, are, with about only one fifth (50 out of 250 species) of their species, useful in littoral zonation that, at about 3 m depth, becomes indistinct. Very rarely, conch shape indicates preferred substrate or life habits. Morphology is more strongly correlated with the history of the species.

Data extracted from observations in the zonation of extant molluscs can therefore be carried into the past as far as a systematic unit can be clearly recognized.

Kurzfassung.

[BANDEL, K. & WEDLER, E. (1987): Hydroiden, Amphineuren und Gastropoden-Zonierung des Karibischen Litorals von Kolumbien. — Senckenbergiana marit., **19** (1/2): 1-129, 48 Abb.; Frankfurt a. M.]

Gastropoden, Käferschnecken und Hydroiden der karibischen Küste von Kolumbien (in der Nähe von Santa Marta) werden charakterisiert und in den ihnen zustehenden Lebensraum gestellt. Einige Arten geben gute Indikatoren ab, die für den Spritzwasser-, den Gezeiten- und

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den Sublitoralbereich typisch sind; andere sind größeren oder kleineren Bereichen zugeordnet, wie etwa einer Rifflagune (groß) oder einem Holzstamm (klein). Eine große Gruppe von Arten kann für eine Zonenuntergliederung des Litorals genutzt werden.

Hydroiden stehen als festsitzende Coelenteraten mit anderen Substrat besiedelnden Organismen in Konkurrenz und spiegeln in ihrer Gestalt und Artenzusammensetzung diese, wie die Art des Untergrundes, die Lichtintensität, die Tiefe und die Strömung wider.

Nur 50 der etwa 250 berücksichtigten Arten der Schnecken und Käferschnecken können zur Litoralzonierung genutzt werden, und Zonen beginnen in 3 m Wassertiefe zu verschwimmen. Die meist ortsbeweglichen Tiere bezeichnen mit ihrer Gehäusegestalt ihren Lebensraum nur selten, und auch das bevorzugte Substrat wird selten abgebildet, dagegen beeinflußt die Entwicklungsgeschichte eng begrenzter taxonomischer Einheiten die Gestalt stark.

Ökologische Daten aus rezenten Beobachtungen, wie der hier vorgestellten, können somit nur soweit in die Erdgeschichte verlagert werden, wie sich kleinere systematische Einheiten verfolgen lassen.

Contents.

Introduction.

Tropical seas show a great density of different organisms living close to each other, especially within the littoral zone. Many types of littoral environments are found close to each other in the area of Santa Marta, at the Caribbean shore of Columbia. Here exposed rock cliffs, deep bays, coral reefs, shallow sand flats, protected bays, lagoons and mangrove are found with a large number of different shore environments. Salinities range from high in lagoons to low in the area of a delta. The fauna at the border between sea and land is arranged in numerous zoned ecosystems in which distinct biocoenoses occur in belts on the shore. In this study we have concentrated on the sessile hydroids and the vagile gastropods and amphineurans to characterize the belts of the shore. To present a coherent picture we have introduced the treated species according to their life habits and placed them in different shore environments. We then ask how environment can be reflected in the shape and construction of the animal living in it. In this way an impression of shapes is presented that can be used when other environments, recent and fossil, are compared and evaluated.

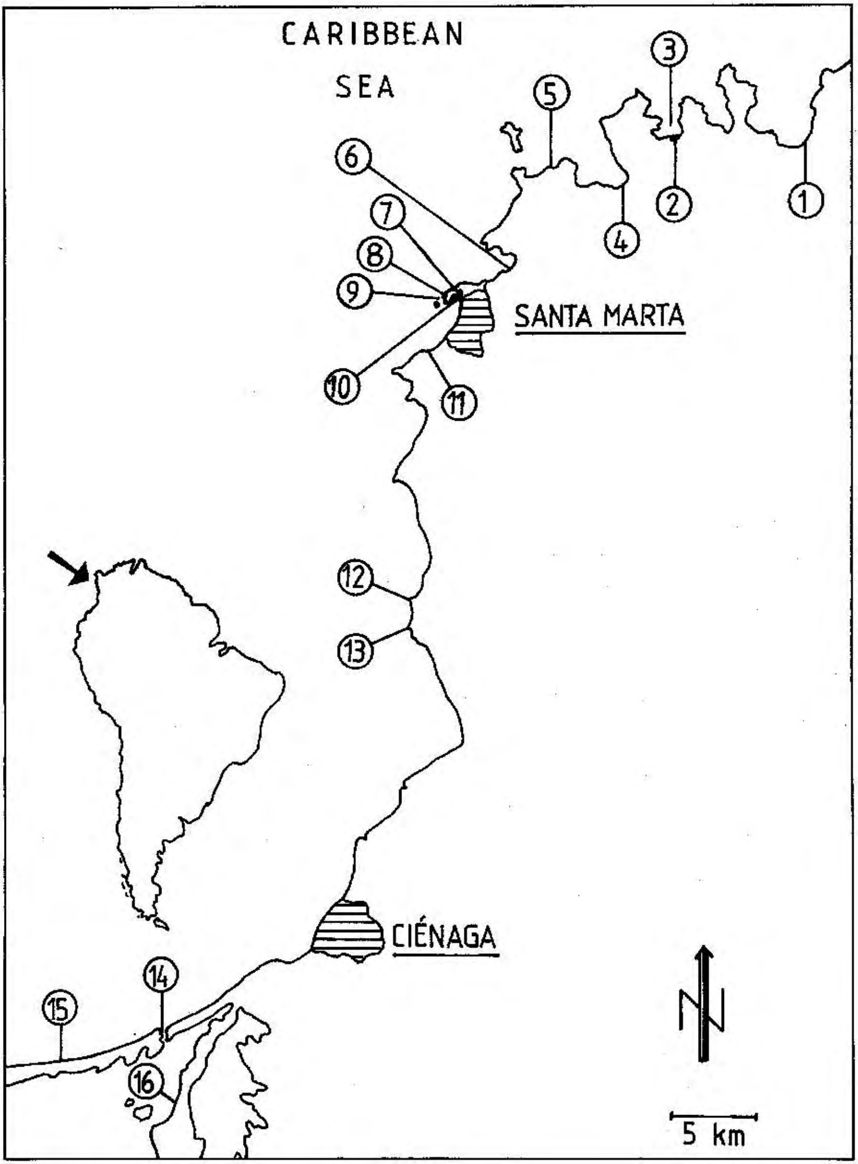
When the faunas of different geographic areas are compared with each other the taxonomy of coelenterates and molluscs is always a little difficult. When recent species are compared with fossil ones the problem increases with the age of the fossils. We have therefore included many simple drawings that can give a more immediate and clear impression. The shape of a colony, skeleton or shell is commonly used to connect it to ecological or paleoecological statements. A comparison of organisms living in the varied surroundings of the Caribbean shore of the area of Santa Marta can be used to check such statements and can, hopefully, help to provide solid data for the interpretation of fossil faunas and prevent erroneous reconstruction and over imaginative theories.

Fig. 1. Map of the region of Santa Marta, Colombia. — Location numbers see text. ▶

Abb. 1. Karte der Region von Santa Marta, Kolumbien. — 1. Sandlitoral in der Bahia de Nenguangue. 2. Lagune in der Ensenada de Chengue. 3. Korallenriff in der Ensenada de Chengue. 4. Sandlitoral in der Ensenada de Concha. 5. Felsklippen an der Playa Brava. 6. Sand- und Geröllitoral in der Bahia de Taganga. 7. Ensenada de Taganguilla. 8. Halbinsel Punta de Betin. 9. Isla Morrito. 10. NW-Pier im Hafen von Santa Marta. 11. Sandlitoral Banco Pobeo der Bahia de Santa Marta. 12. „beach rock" Punta La Loma am Flughafen Simon Bolivar. 13. Punta Brava, Granitfelsen im Sandlitoral. 14. Mündung der Ciénaga Grande de Santa Marta. 15. Isla de Salamanca. 16. Mangrovenufer in der Ciénaga Grande de Santa Marta.

Geographic Setting and Climatic Conditions.

The ancient town of Santa Marta on the Caribbean coast of Columbia has a natural harbour that lies on the margin of a mountainous area (Fig. 1). In the North the mountain range of the Sierra Nevada de Santa Marta descends to the sea. Its



slopes form steep cliffs which are more or less exposed to the tides of the open sea. Deep valleys that formed during glacial times were flooded and now form deep bays, which become increasingly wider and shallower from the north to the south. These bays are Bahia de Nenguange (1), Ensenada de Chengue, lagoon (2) and coral reef (3), Ensenada de Concha, beach and drop (4), rock cliffs of Playa Brava (5), Bahia Taganga with Taganga village (6), the Bahia de Santa Marta with Ensenada de Taganilla (7), peninsula of Punta de Betin (8), Isla Morrito (9), NW jetty of the harbour of Santa Marta (10) and the sandy Banco Pobea in the bay (11). South of Santa Marta sandy beaches predominate and are only rarely interrupted by rocky cliffs such as at Punta Brava (13) and by beach rock exposures such as is the case at Punta La Loma (12), both localities close to the airport of Santa Marta Simon Bolivar. The area south of the town of Cienaga belongs to the delta of the Rio Magdalena and consists of alluvial deposits of sandy, muddy and organic composition. Mangrove forests surround saline, brackish or fresh water ponds lagoons and canals as well as river mouths. The whole area of the delta lies just above or just below mean water sea level and, to a large extend, is inundated by floods of the Rio Magdalena periodically once or twice each year. A large shallow lagoon of 450 square kilometers water surface, the Cienaga Grande de Santa Marta (16) is present, is connected to the fresh water runoff of the Sierra Nevada and the Rio Magdalena. It opens to the sea with a "Bocca de la barra" (14). The Caribbean current, and moving along the shore of the long beach bar of the Isla de Salmanca (15) continously brings fresh sea water that is washed into the mouth of the lagoon by each tide, thus creating estuarine conditions.

From December to March (April) and from July to August the climate is dry and strong trade winds blow, transporting surface water in the direction of the open sea. In the large area between Cienaga, Santa Marta and up to 100 km east of Santa Marta cool water of the deep ocean rises (upwelling) and water temperature drops almost to 22°C in December. In the large Cienaga Grande, evaporation and wind bring the water temperature to 27°C in this time. From April to June and from September to November the rainy seasons terminate trade winds and water warms up considerably, to about 29°C in the open sea and 32 to 34°C in the Cienaga Grande lagoon. Air temperature also varies from about 27°C at trade wind time to 35°C with slack winds. The salinity in the open sea around Santa Marta and in the bays varies between 35.5‰ and 37‰, while in the Cienaga Grande the water can be fresh during Rio Magdalena floods and saline to an extent of 40‰ during extended dry periods. Near Santa Marta two strong currents meet, one of which comes along the coast from Panama (West to East), the other from the Guajira peninsula (from NE to SW). The oxygen content of the open sea is therefore stable (6 ml/l) and acidity ranges from pH 8-8.2. In the lagoon of the Cienaga Grande these values are lower for the oxygen (4 ml/l) and more variable in case of the acidity (7-9 pH7).

Zonation of the Shores.

A differentiation of the shore area into Supra-, Eu- and Sublittoral zone can be carried out simply by looking at the tidal range (RIEDL, 1964). Within this range further differentiations are more difficult to develop. Measurements of abiotic factors over a long range of time could provide data. A more simple way of approaching the problem is by analysis of the fauna and flora. A detailed analysis of the flora of the rocky shore has been carried out in the geographically close area of the Dutch Antilles, Curacao and Aruba, by VAN LOENHOUD & VAN DE SANDE (1977). This zonation and BRATTSTRÖM's (1980) study can be used on the rocky shores of Santa Marta.

The upper limit of the sublittoral zone coincides with the characteristic bore holes (pits) of the sea urchin *Echinometra lucuntor.* This zone and the infralittoral margin (fringe) are characterized by dense algal turf consisting of brown and red algae. Here short Sargassum may be attached to the rock.

The Eulittoral (Mesolitoral) zone is narrow, since tidal range is small amounting only to about 30 or 40 cm. Still the rocky eulittoral can be subdivided into a lower and an upper belt. The lower belt is characterized by crusts of *Lithothamnium* and is tinted in the pink and white colours of these crust-forming calcareous algae. The upper eulittoral belt, in contrast, is covered by creeping filamentous green and blue green algae.

The boundary to the supratidal zone also shows up well due to a colour change from green to black. Coccoid blue green and filamentous algae form a thin film on the rock. Further up on the rocky shore these algal covers are thinner and rock is yellow to light brown. This zone extends to the supralittoral margin, where salt erosion is common. VAN LOENHOUD & VAN DE SANDE (1977) and BRATTSTRÖM (1980) discussed the literature on rocky shore zonation in detail, so that we need not go into the subject in detail.

Rocky shore and mangrove are populated by supratidal gastropods and intertidal hydroids, whereas gastropods can be found on sand and mud shores from the eulittoral downwards, hydroids live only below low water line. In the mangrove the bushes and prop roots take the place of the supratidal cliff. The intertidal zone of the eulittoral equals the leaf-littered bottom, and prop roots and the infralittoral fringe lies in the mangrove lagoons. The hight of the eulittoral zone is even less than 30 cm at this point.

Materials and Methods.

As our research-area we selected sections of the coast that differed from each other in the composition of their substrate, the inclination of the shore, the orientation in regard to sun exposure and wave action. Other factors were also included, as for example the presence of coral reefs or mangrove forrest.

The animals were collected by hand with the aid of snorkeling and shallow scuba diving. A few dredge wholes have been included. Characteristic biotopes have been documented by underwater photographs. Sections were drawn in the field and numerous excursions supplied further data. Observations were carried out for 16 months continuously and supported by additional later observations. Water movement was registered with floating bodies. Light was measured via interference-filter and with a method developed for the study. Vertical sections were measured with an Oxygen temperature device (GRASSHOFF).

We searched for species and morphotypes that (a) are common (b) show a relatively narrow area of distribution, (c) react to differences of the environment in regard to their shape.

Gastropods of the Littoral Zones and their Mode of Life.

The snails listed here are arranged in systematic order that follows the classification adopted by ABBOTT (1974). In this book on ‚American Seashells' a description of almost all species can be found which are mentioned here. Those with a number at the end have been included in the figures as drawings. A short characterization of their mode of life is presented as it has been observed in the sea near Santa Marta and in aquaria in the marine station of Santa Marta.

Archaeogastropoda.

Fissurellacea.

The limpet-like *Hemitoma octoradiata* (GMELIN 1791) (6) lives on rock in 0.5 to 2 m depth within the infralittoral zone. While young individuals of *Hemitoma* prefer the lower, shaded sides of rocks, adult individuals dwell on the sunlit rock-surfaces. The shells of older individuals, therefore, are encrusted with calcareous algae and are well camouflaged, merging with the surrounding rocks that are covered by the same algae. *Hemitoma* feeds on calcarous algae. Outside of times with intense radiation of the sun it continuously scrapes crusts from the rocky substrate.

Diodora listeri (ORBIGNY 1842) (3) also feeds on algae. It selects non-calcareous, soft algal moss on rocks, boulders and larger pebbles within the infralittoral fringe and from 0.5 to 3 m depth. *Diodora cayenensis* (LAMARCK 1822) lives like *D. listeri* on single rocks, pebbles, fragments of coral and the dead lower side of coral colonies resting on sandy or detritus covered loose substrate at the edge of coral reefs or within the reef between corals. It lives, however, in the deeper infralittoral zone from 2 m onwards and was commonly observed between 3 and 10 m depth. *Diodora variegata* (SOWERBY 1866), in contrast, lives in shallower water within the infralittoral fringe to 1 m depth, on the underside of pebbles and rocks.

The four members of the genus *Diodora* prefer soft food consisting of algal tufts and moss as well as small animals encrusting sunlit or shady rocks and living among the algae. A fifth species of this genus *Diodora viridula* (LAMARCK 1822) settles only on the shady sides of rocks and jetty piles as well as the lower, submerged parts of boats and other permanently floating objects.

Lucapina suffusa (REEVE 1850) covers most of its conical shell with a fleshy mantle and lives exclusively on the lower shaded side of rocks and boulders. In the same type of environment the smaller *Lucapinella* cf. *limatula* (REEVE 1850) (= *Diodora wetmorei*, FARFANTE 1945) is found which covers only part of its outer shell with the mantle. Both species are quite mobile and feed mainly on sponges and, probably, also on other colony-forming animals that encrust rocky surfaces in 0.3 to 3 m of depth within the infralittoral zone. *Lucapina* shows a large variety of mantle pigments ranging from brightly orange to dull brown, from spotted to greyish opaque.

Fissurella nodosa (BORN 1778) (5) dwells on rock-cliffs in the intertidal zone. Its shell is usually strongly encrusted with calcarous algae of the same type that it scrapes from rock surfaces in its strongly wave exposed environment that is continuously washed by clear water. *Fissurella nimbosa* (LINNÉ 1758) prefers about the same position in the intertidal zone as *F. nodosa*, but the two do not occur together. It settles on the surface of large granitic boulders with smooth surface that can be found isolated in an otherwise sandy surrounding. Here waves washing up continuously bring sediment loaded water with them. *F. nimbosa* moves around in the middle intertidal zone that is here covered with tufts of red and brown algae and feeds on them. This area lies above the whitish crusts of coralline alga of the lower intertidal zone and below the barnacles covering the upper intertidal zone.

Fissurella angusta (GMELIN 1791) and *Fissurella barbadensis* (GMELIN 1791) (4), in contrast, live just below the intertidal zone. Individuals of both species are very similar to each other and can be differentiated best by a brown callus line on the inner apical side of the shell, by the colour of the body and by the number of tentacles protruding from the upper side of the head. Shells of both species are usually strongly encrusted. Individuals found on the shaded sides of rocks and boulders are often covered by colourful sponges, tunicates, bryozoans and coelenterate colonies. Individuals attached to the sun-exposed side of hard substrates are covered by algal crusts and tufts. Crusts and overgrowths often extend from the shell surface onto the surrounding substrate without interruption. This indicates that individuals of both species of *Fissurella* do not frequently change their living place. They do not feed by grazing or scraping but obtain their food by filter feeding. Below their foot and shell the rock is free of algae, in contrast to the resting places of the other members of the fissurellids. When detached from their holdfast the limpets moved actively demonstrating that they can change their position on the rock if conditions become unfavourable. *F. angusta* is so well camouflaged that only the orifice with a rim of the mantle extending from it may betray its position on the surface of pebbles, reef-rock and rocky cliffs. On strongly exposed cliffs it prefers the holes excavated and inhabited by sea-urchins (*Echinometra*) as living place. *F. barbadensis* is fitted into shallow cavities on the rock or the concrete of the harbour jetties, and is never seen moving about like the other inhabitants of these environments with a cap-like shell (*Acmaea, Hemitoma, Siphonaria*).

The small *Emarginula pumila* (A. ADAMS, 1851) lives a very hidden life among *Acropora* thickets or the crevices in the coral reef and feeds on crust-like sponges.

Patellacea.

The patellids *Collisella antillarum* (SOWERBY 1831) (7) and *Acmaea pustulata* (HELBING 1779) are found on rocky substrates ranging from the central portion of the intertidal zone to a depth of about 1 m in the infratidal fringe. Only large individuals can remain on the upper, exposed surfaces of rocks while individuals of all sizes are present on the lower, sun- and wave-protected sides of the rocks. Commonly one or two individuals of either one or both species live on the horny operculum of the large top shell *Cittarium*. A variety of *A. pustulata* lives on the blade-like leaves of the turtle grass, but these individuals never reach a large size. This form may represent a third species. *Acmaea* and *Collisella* feed on calcareous algae that are scraped from various substrates.

Trochidae.

Calliostoma sarcodum DALL 1927 is fairly common on the underside of rocks within the infralittoral fringe, from low water level to about 1 m of depth. It feeds on soft, non-skeletal, crust-forming, colonial animals such as tunicates. Prey is brushed off its holdfast with the help of the delicate, many-cusped teeth of the radula. *Calliostoma* can creep rapidly. When detached from its holdfast it can twist into an upright position rapidly. This twisting motion is also used for escape from a star fish or a carnivorous gastropod like *Fasciolaria*. When *Calliostoma* senses an enemy it detaches from hard substrate, usually the underside of a rock, falls down landing on the back of its shell. It then rolls sideways away from danger with repeated rapid pushes of the foot. It then reattaches itself to be the substrate with the sole of the foot and crawls away rapidly.

Cittarium pica (LINNÉ 1758) (8) is a large top shell that prefers rock-cliffs. It feeds on non-calcareous algae growing in the splash zone to about 1 m below it. Fully wave exposed rock cliffs facing the open Caribbean Sea are favoured. In areas where *Cittarium* is not collected by the local population to be used in chowders (boiled in hot water, extracted from the shell, eaten mixed with rice and spice) large individuals are common with individuals of all sizes. Near villages, they survive only in the shelter of deep rock clefts and overhangs. Escape reactions of *C. pica* can be observed by suddenly shading an individual The snail drops from its holdfast, falls from the rocky cliff and is washed below water by the next waves. When the animal retracts into its shell it excretes an opaque liquid that is spread by the currents and waves and warns other individuals of this species living close-by. These individuals begin to crawl around rapidly until they also detach from their holdfasts. One individual can in this way alarm a whole population living within a few meters of a rocky shore in the time 3-4 waves need to wash the rocks.

Four species of the genus *Tegula* (9-12) live on hard substrates within the intertidal zone and the infratidal fringe. They feed on tufts, crusts and mosses of non-calcareous algae. They prefer rocky substrates outside of areas with very heavy surf and they avoid cliffs. During daylight at times of intense sunlight individuals cluster in large groups on the underside of rocks. At times of low sunlight or at night, the snails leave their resting place and start feeding on the rocky surfaces with closely placed scrapes of the radula forming a tightly meandering path. *Tegula viridula* (GMELIN 1791) (9) is abundant on rock-strewn beaches or pebble beaches below the tide level. *Tegula excavata* (LAMARCK 1822) (10) prefers the intertidal zone on the same beaches. The large populations of this species migrate up and down with the tides. Both species prefer beaches where sand is found between the rocks and pebbles. *Tegula fasciata* (BORN 1778) (12) replaces *Tegula viridula* in reef lagoons where it may be common down to depth of 3 m. In clear lagoonal environments it feeds on algal growths covering turtle grass and rocks. *Tegula lividomaculata* (C. B. ADAMS 1845) (11) tolerates water with much suspended sediment in it, whereas the other three species of *Tegula* live only in clear water. *T. lividomaculata* is found within the intertidal zone and the infratidal fringe down to 1 m depth on rocks covered with green and reddish brown algae that are caked with sand. *Tegula* can not recover its holdfast to a hard substrate when it falls upside down onto pure sand, as could commonly be observed in the experiment.

Cyclostrematidae.

Arene tricarinata (STEARNS 1872) and *Arene cruentata* (MÜHLFELD 1829) are small, depressed turbinate, thick-shelled trochids that live in 0.5 to 1 m depth under rocks. They are found in the turtle grass environment, and below pebbles or small rocks close to coral reefs or patch reefs. Individuals of both species are rare; they feed on growths and crusts of minute algae.

Turbinidae.

Turbo castanea (GMELIN 1791) scrapes algae from shallow rocks in quiet bays and lagoons. The dominant sediment here is sand and mud that has to be periodically crossed to reach a new rock. *Astraea phoebia* (RÖDING 1798) is associated with, but less common than *Turbo*. In addition, it can be found on hard substrates in the turtle grass environment, on large rocks but also the large valves of *Pinna* and *Atrina*. The thick shelled *Astraea caelata* (GMELIN 1791) (13) prefers the wave-washed algal ridge of the coral reef within the infralittoral fringe but is also present between coral growths and on both sides of the ridge of the reef crest. It may also be present on exposed rocky cliffs in 1-3 m depth but in fewer numbers than in the coral reef environment. The long-spined *Astraea phoebia* (RÖDING 1788) can be found among coral rubble in the reefs, and here also *Astraea tecta* (LIGHTFOOT 1786) lives but usually in slightly deeper water. Individuals of the genera *Turbo* and *Astraea* graze algae from hard substrates with closely spaced rasps of the radula arranged in a row that froms a densely meandering path exploiting the organic covers of the rock surface quite intensively.

Phasianellidae.

The four species of the genus *Tricolia* (14-16) feed on minute algae. *Tricolia affinis affinis* (C. B. ADAMS 1850) (15) forms mass populations on growths of brown *Sagassum* attached to rocks and cliffs in the intertidal zone or the infratidal fringe. The populations change periodically in density with fewest individuals found in the rainy season when the water is commonly turbid, and extremely large populations are found during the dry seasons, especially during the months of September and October, when the water is clear. *Tricolia tessellata* (POTIEZ & MICHAUD 1838) (14) may also live on *Sargassum* in small numbers but it is more commonly found on the underside of rocks and pebbles in the infralittoral fringe. *Tricolia bella* (M. SMITH 1937) (16) can also be encountered here but more commonly lives on the blade-like leaves of the turtle grass within the infralittoral zone in 0.5 to 2 m depth. *Tricolia affinis cruenta* ROBERTSON 1958 takes the place of *T. bella* on the thinner, rounder and more slender leaves of the eel-grass growing in 3-5 m of depth.

Neritacea.

The Neritidae (17-22) are a very conspicuous group of littoral gastropods with clear preferrences regarding their specific habitat. The four representatives of the genus *Nerita* (17-20) scrape algae and other encrusting plants from rocks and from mangrove wood with the help of very strong and mineralized teeth of the radula. *Nerita tessellata* GMELIN 1791 (20) lives in the lower intertidal zone and the infralittoral fringe on rock and pebble beaches that are exposed to little or moderate wave action. When living on the roots of mangrove bushes, members of this species remain under water. The range of *Nerita fulgurans* GMELIN 1791 (18) overlaps with that of *N. tessellata* in the lower intertidal zone but continues up into the zone of continuously wet but not continuously submerged rocks. On mangrove wood *N. fulgurans* is found both above and below the water surface. *Nerita versicolor* GMELIN 1791 (17) lives on rocky substrates in the uppermost intertidal zone but prefers to live above the surface of the water within the splash zone. The same area of the lower supralittoral fringe is also settled by *Nerita peloronta* (LINNÉ 1758) (19) which on exposed cliffs penetrates higher on the supralittoral fringe than *N. versicolor*. Populations of both species occur together on rocks and cliffs above the tidal level and near splash pools and spray pools. Individuals of *N. peloronta* may grow to a larger size than those of *N. versicolor*, and only the very large individuals occur highest on rocky cliffs.

Neritina virginea (LINNÉ 1758) (21), in contrast to the fully marine species of the genus *Nerita*, prefers environments with brackish water, even though members of this species will survive well under marine conditions in very protected environments, as for example the artificial basin of the yacht harbour at Santa Marta-Rodadero. Large populations with countless thousands of individuals are found on muddy and sandy bottoms as well as on mangrove roots and stems within the tidal zone in estuarine areas. The shell of this species is extremely variable in pattern of ornamentation and, to a lesser degree, in coloration which may include purple, yellow, green, brown, and black. A very similar species *Neritina clenchi* RUSSEL 1940, lives within the mangrove forrest on decaying leaves that litter the muddy bottom and on the beach of mangrove ponds. Here salinity is usually brackish. Both species of *Neritina* feed on fungi, algal crusts and decaying plant matter.

Smaragdia viridis (LINNÉ 1758) (22) is well camouflaged by the green colour of its shell on its living substrate of the leaves of turtle grass. Fresh leaves of this marine angiosperm also forms the food of *Smaragdia*. The leaves of *Thalassia* consist of two cell layers and are patterned with longitudinal and transversal veins. *Smaragdia* feeds on the cells of one layer between the veins by scraping rectangular grooves. The small limpet-like snail *Phenacolepas hamillei* (FISCHER 1857) (23) with a whitish translucent shell, also lives on the leaves of the turtle grass but is much less abundant.

Mesogastropoda.

Radulae of almost all species considered in this account have been described and illustrated by BANDEL (1984).

Ampullariidae.

The species of both *Ampullarius* (24) and of *Marisa* (25) are restricted to freshwater and are good indicators of the dividing line between fresh and brackish water since they are very common and large sized. *Ampullarius monticolus* (VERNHOUT 1914) lives in running freshwater and was found in the lower reaches of the Rio Cordoba before it enters the zone of the freshwater swamps that surround the brackish lagoon of the Cienaga Grande towards the mountains of the Sierra Nevada. *Ampullarius porphyrostomus* (REEVE 1856) (24) and its close relative with an almost planispiral shell *Marisa cornuarietis* (LINNÉ 1758) (25) live within the stagnant water of these swamps. Both species can be found in any freshwater pool or river arm with slow moving water within the delta of the Rio Magdalena and along the coast. *Ampullarius* and *Marisa* feed on freshwater plants as well as fresh or decaying plant material. *A. porphyrostomus* produces large, white very conspicuous egg masses that are attached to stalks and stems of water plants at least 10 cm above the water surface (BANDEL 1976). These durable, calcium-carbonate encrusted egg masses indicate the dividing line between brackish and fresh water and can be regarded a good biological marker of this salinity change.

Littorinacea.

The periwinkles (26-32) are typical gastropods of the tidal and subratidal zones. Stems and branches of bushes and trees in the mangrove forrest under fully marine, lagoonal and estuarine conditions are settled by *Littorina angulifera* (LAMARCK 1822) (30) usually in great abunance. This species penetrates deeper into the estuarine area with its continuous periodical changes between normal marine and brackish water than *Littorina nebulosa* (LAMARCK 1822) (30). Both species prefer wood as substrate even though they may be found on concrete harbour pilings or larger rocks strongly overgrown with filamentous algae, usually near the entrance to estuarine areas. *L. nebulosa* feeds on the wood of larger stems that have drifted to shores and become anchored within the intratidal area. It devours the decaying wood itself, and may be present on shores with very strong surf as well as on fairly quiet beaches. *L. angulifera* most commonly is found on wood of living mangrove trees, where it crawls up and down on the stems and roots independently from rising or falling water of the tides and from spray or waves.

The other periwinkles prefer rocky substrates. The small *Littorina meleagris* (POTIEZ & MICHAUD 1838) (28) likes pebble beaches in moderately agitated waters, where it feeds on algal tufts and mosses just below wave line. With rising water the population of *L. meleagris,* which normally consists of numerous individuals, migrates upward and with falling water they migrate downward and are, therefore, always browsing the rock surfaces just below water level. Protected tidal pools with often renewed water and splash pools of cliffs exposed to strong wave action are also settled. At high tide the populations of *L. meleagris* reach the lower members of the populations of *Nodilittorina ziczac* (GMELIN 1791) (26), which live within the splash and spray zone. On exposed cliffs, *N. ziczac* is found in the lower supralittoral fringe while *Nodilittorina interrupta* (C.-B. ADAMS 1847) (27) settles the central and upper part of the supralittoral fringe. On less exposed cliffs and rocks, the zones settled by these species move closer together and populations mix. Individuals of both species have to tolerate great heat and much desiccation, and are forced to long periods of inactivity during the calm months of the rainy period, when their living environment is not moistened by the sea. *Nodilittorina tuberculata* (MENKE 1828) (31) lives in about the same environment as *N. interrupta* within the blackened zone but prefers smoother and less inclined rocky substrates and is commonly found on the upper rock cliff platform with slash and spray water pools. *N. tuberculata* may roam about within the warm and hypersaline pools whereas *N. interrupta* usually avoids them except for their wet rims. *Cenchritis muricatus* (LINNÉ 1758) (32) can tolerate more dryness than any of the other marine gastropods in the area and lives highest in the supralittoral zone. In quiet lagoons, in contrast, it may be found only a few centimeters above water level but may be wetted only when extremely high swells reach these protected beaches. All the rock-dwelling periwinkles scrape algal custs and other plant crusts from rocks, and also erode considerable amount of rock material in their search for food.

Rissoacea.

In ponds of fresh water behind beach walls, the small hydrobiid snail *Assiminea succinea* (PFEIFFER 1840) (33) occurs in great numbers, feeding on diatoms and other minute algae as well as on fresh and decaying plant particles. This species lives primarily in pools and lakes of fresh water but brackish water is tolerated to some degree. *Assiminea* reaches maturity after only a short period of growth, and therefore mass populations can establish themselves within a few months. For example, when the very large shallow brackish lagoon of the Cienaga Grande became fresh because of high water from the Rio Magdalena large populations of *Assiminea* became established rapidly, only to be exterminated latest after 4 months time when brackish conditions returned.

Dense algal turf of many brown and red algae within the infralittoral margin and just below it but also algal thickets growing on dead branches of coral within the coral reef of the *Acropora* thickets are settled y a number of rissoids like *Rissoella caribaea* REHDER 1943, *Zebina browniana* (ORBIGNY 1842) several species of *Rissoina, Barlecia* sp., *Amphithalamus* sp. and *Cingulopsis* sp. The last three also occur on *Sargassum.* All these rissoids are common only periodically and their dead shell are ubiquitous in many littoral sands, while living animals are less commonly found. Their food consists of minute particles which they collect from the algal tufts.

Caecidae.

The tiny, tusk-shaped species of the genus *Caecum* (34, 35) feed mainly on diatoms and other unicellular algae. The minute gastropods climb in search for food among mosses and tufts of algae on hard substrates as well as thickets of filamentous green algae covering hard surfaces and soft substrates. They occur most commonly from the base of the intertidal zone to a depth of 5 m. *Caecum pulchellum* (STIMPSON 1851) (34) is more common on soft substrates, whereas *Caecum nitidum* (STIMPSON 1851) (35) is more common on hard surfaces. Aside from these two species there is a number of other species of *Caecum* found.

Turritellidae.

Turritella variegata (LINNÉ 1758) (36) lives within muddy, soft sediment at water depth greater than 2 m. The elongate turret shell is oriented parallel to the sediment surface, but completely hidden below it. Through a pit in the sediment above the operculum, sea water is sucked in and planktonic and suspended food is extracted. If undisturbed, *Turritella* leaves its feeding and resting place only once a year, for spawning (BANDEL 1976).

Architectonicacea.

Architectonica nobilis (RÖDING 1798) (37) is active at night. In daytime it rests within soft sediment between the root system of *Thalassia* in the turtle grass meadows at 3-6 m depth with the aperture pointing upwards, so that head and foot are situated just below the sediment surface. *Architectonica* feeds on sea anemones by piercing the base of the polyp with its proboscis and sucking the tissue of the coelenterate until it collapses and dies. Single polyps of anemones live attached in large numbers on the leaves of the turtle grass and other substrates found in this environment.

Epitoniidae.

Epitonium lamellosum (LAMARCK 1822) feeds in a very similar way as *Architectonica.* Near Santa Marta it was encountered only in deeper water and on muddy substrates, but enters the shallow Cienaga Grande when this lagoon has reached almost fully marine salinity.

Vermetidae.

Two members of the genus *Petaloconchus* (38), with irregular worm like tubes, live attached to rocks. *Petaloconchus varians* (ORBIGNY 1841) is a typical representative of the intertidal fauna and *Petaloconchus erectus* (DALL 1888) lives in the protection of the crust forming sea anemone *Palythoa caribbaea* in water 1-2 m deep. *P. varians* lives attached to cliffs and boulders where the surf is strong and supplies a continuous stream of food particles for this sessile filterfeeding snail. It is concentrated in small and large channels through which breakers wash into tidal pools and onto tidal platforms and from them back to the sea. Many individuals together can form small reef-like bodies attached to the platform of breaker terraces in the central intertidal zone. Here they co-occur with byssally attached bivalves (*Isognomon* and *Brachidontes*). In these reef-like mounds the tubes of the shells of a number of individuals support each other and point upwards. *P. erectus* also forms upward-pointing tubes, but these are isolated because they grew as scattered individuals within a dense crust of the large sized *Palythoa.* Only the upper end of the tube extends above the zoantharid crust into the free water, from which food is filtered.

Planaxidae.

Two members of the genus *Planaxis* (39, 40) live in the intertidal zone of rocky shores with light to moderate wave action. Individuals of both species migrate up and down with the tides. Both species avoid sandy bottoms as well as cliffs, and settle beaches covered with pebbles, boulders or rock debris. Here they graze algal mosses and mats from the surface of hard substrates without chisseling into the rock as is the case in most rock-dwelling periwinkles and neritids. *Planaxis nucleus* (BRUGUIÉRE 1789) (40) feeds on rocks which fall dry with each retreating wave and are wetted with each coming wave. *Planaxis lineatus* (DA COSTA 1778) (39), in contrast, remains just below wave line so that it is almost continuously submerged. *P. lineatus* more than *P. nucleus* avoids sunshine and remains on the shaded sides of rocks during daytime, while the latter during continuous action of the surf feeds even when fully exposed to the sun.

Modulidae.

Modulus (41) with a solidly build trochoid shell, grazes algae from hard substrates. *Modulus modulus* (LINNÉ 1758) occurs at 0.2 to 2 m below the normal low tide, either on rocks with muddy or sandy substrates between them or on the root systems and the leaves of turtle grass. Populations consist usually of numerous individuals, while *Modulus carchedonius* (LAMARCK 1822), in contrast, is rarely found in pools with slightly brackish water, as for example the artificial harbour of Santa Marta-Rodadero. *M. carchedonius* is not present in swamps and lagoons of the mangrove.

Cerithiidae.

The three species of *Cerithium* (42-44) are herbivorous grazers and collectors of algae and other plant matter. *Cerithium lutosum* (MENKE 1828) (44) was found only in the Ensenada de Chengue. Here it lives with countless thousands of individuals within a shallow, warm, somewhat hypersaline lagoon. Large populations are found on *Halimeda* or on the roots of mangrove bushes. Others are scattered on the muddy bottom. *C. lutosum* feeds on small algae, mainly diatoms, which cover the muddy substrate and all plants within the lagoon. Near the shore in the shallow intertidal zone of the reef lagoon, numerous individuals of *C. lutosum* feed on decaying turtle grass. *Cerithium atratum* (BORN 1778) (43), in contrast, lives in most sea grass meadows as well as on muddy and sandy bottoms in 1-5 m depth. In calm bays it may live in the intertidal zone even where it is rocky, but it avoids this zone near beaches with more agitated water. Often groups of a few tens of individuals migrate across sandy or muddy bottoms grazing like flocks of sheep from algae growing on the surface and on living and decaying plant material in the uppermost millimeters of the sediment. *C. atratum* and *Cerithium litteratum* (BORN 1778) (42) co-occur within the shallow turtle grass environment. Otherwise *C. litteratum* prefers hard substrates that are covered with dense algal tufts ranging from about 1-4 m depth. Here adult populations may exceed several hundred individuals per square meter.

Diastoma varium (PFEIFFER 1840) (45) periodically occurs in very large populations in extensive algal thickets that cover all types of substrates in 0.5 to 2 m depth in protected parts of the bays during periods of the year with clear water. Smaller populations of this small and slender snail can be found throughout the year in all algal growths in shallow water. The very similar species *Finella dubia* (ORBIGNY 1842) (46) also occurs as extensive and large populations in thickets of filamentous algae on muddy substrates during periods of calm clear water. When these mats disappear during periods with turbid water and incoming larger swell, much smaller populations are found on muddy substrates from just below the intertidal zone to about 10 m depth.

Litiopa melanostoma (RANG 1829), another small cerithid lives mainly on Sargassum and is found throughout the year. On these weeds *Alaba incerta* (ORBIGNY 1842) (48) is a characteristic small cerithid usually present with numerous individuals of all sizes. Large tree-like *Sargassum* that is rooted in water a few meters deep and extends to the surface continuously branching and widening in diameter may grow within the Ensenada Granate and in other bays north of Santa Marta during few months each year with clear water. During these short periods huge populations of *Alaba* with many millions of individuals form. During the rest of the year, when the *Sargassum* trees have become detached from their holdfasts and drifted away, no living *Alaba* can be found within this area; the only surviving populations are on *Sargassum* left within the intertidal zone and the infralittoral fringe on cliffs and boulders. *Diastoma, Finella, Litiopa* and *Alaba* are herbivorous animals collecting unicellular algae, sometimes with the help of mucus that is secreted by their foot. All of them may reach maturity after a very short period of growth, and thus can form short-lived mass populations.

Cerithiopsidae and Triphoridae.

Species of *Cerithiopsis* (47), *Triphora* (49) and *Seila*, which are small, slender ceriths, feed on sponges mainly; *Triphora turristhomae* (HOLTON 1802) lives in shallow water on rocks encrusted with yellowish and white sponges. The snail feeds on the tissue of these sponges with only at most the top of the apex exposed above the sponge colony. *Triphora nigrocincta* (C. B. ADAMS 1839) prefers to feed on yellowish sponges that grow on rocks in 0.5 to 1.5 m depth in calm bays. *Seila adamsi* (H. C. LEA 1845) is found on the underside of rocks and coral fragments, often together with *Triphora turristhomae*. *Seila* feeds on sponges and also perhaps on tunicates. *Cerithiopsis emersoni* (C. B. ADAMS 1838) (47), like *Triphora nigrocincta*, feeds on sponges attached to the underside of rocks at about 1 m depth. Several other species of *Cerithiopsis* and *Triphora* live wherever crust-forming sponges are present. It seems likely that single species of these snails feed only on specific sponge species.

Melanellidae.

Small elongate shells with glossy surface belonging to the melanellid genera *Eulima* and *Balcis* are common in all sands of the infratidal region. Living individuals can be found only associated with their hosts. They are parasites on holothurians, starfish and sea urchins.

Hipponicidae and Calyptraeidae.

Cap-shaped mesogastropods are represented by species of *Hipponix* (50), *Cheilea, Calyptraea* (51), *Crucibulum* (52), and *Crepidula* (53, 54). All of them feed by filtering particles from the water. Only *Hipponix antiquatus* (LINNÉ 1767) (50) is firmly attached to its substrate, at the adult stage, with a calcareous plate. They are found in 0.5-2 m depth on rock surfaces sheltered by other rocks. *Hipponix*, thus, filters food from water washed between the rocks of the boulder and rock strewn intertidal fringe. It is restricted to shores where interspaces between rocks are washed continuously by strong currents but where surf is not strong enough to move the rocks themselves.

Cheilea equestris (LINNÉ 1758) lives attached to the upperand lower surfaces of rock or other hard substrate in 0.5 to 1 m depth. The edge of its cap shaped shell is fitted into the substrate surface and the outside of the shell is overgrown with algae or other crust-forming organisms like those covering the surrounding rock. The snail will usually remain on its once chosen place unless fine sediment threatenes to bury it. *Cheilea* prefers non-moving objects for attachment, but *Crucibulum auricula* (GMELIN 1791) (52) settles on rocks as well as on larger shells of living gastropods. Within the bay of Taganuilla for example, *Latirus infundibulum* is used as host, while in the Ensenada Cañaveral, *Strombus gigas* is a host. Individuals attached to the shell of *Latirus*, because of the very limited space available, have high, deep cup-like shells, while those attached to the larger shell of *Strombus* or those attached to rocks have much flatter, shallow, cap-like shells. *Calyptraea centralis* (CONRAD 1841) (51), in contrast to *Cheilea, Hipponix* or *Crucibulum,* usually has a very regular, smooth cap-like shell. It attaches to mollusc shells, mostly the large valves of dead lamellibranchs lying on muddy bottom or fine sand deeper than 5 m.

Crepidula plana (SAY 1822) (54), after metamorphosis, settles on gastropod shells that are being lived in by hermit crabs. The milky-white convex to concave slipper shell is attached to the inner side of the outer lip of the gastropod shell, which belonged to one of the larger species of gastropod present within or near the area. *C. plana* profits as a commensal from this location by deriving food from the inhalent and exhalent currents continuously generated by the crab. Thus the snail profits from food particles suspended around the crab when it is feeding, from the feaces of the crab and from food particles suspended in the water itself. The hermit crab transports *Crepidula plana* over large areas extending from the intertidal zone to depths of 15 m. Usually at least two *Crepidula* individuals are attached to the shell of each hermit crab — a larger female and, close beside it, a smaller male. Many larger living snails carry individuals of *Crepidula convexa* (SAY 1822) (53) attached to the outer surface. The preferred site for attachment on the shell is close to the outer lip. In the turtle grass lagoon of the Ensenada de Chengue the shell of *Tegula fasciata* serves as the host, while in the restricted mangrove lagoon of the same bay *Cerithium lutosum* is the host. On beachrock close to the airport of Santa Marta (Punta la Loma), *Tegula lividomaculata, Leucozonia nassa* and *Fasciolaria tulipa* are hosts for *C. convexa.* In the bay of Taganilla, *Latirus infundibulum* and *Cerithium atratum* are hosts. Usually there are at least two individuals attached to a host, a larger female and on its shell or at its right side a smaller male. C. *convexa* is restricted to the intertidal zone and the infralittoral fringe in habitats ranging from very calm slightly hypersaline lagoon to moderately exposed rock cliffs, from muddy substrate to pebble beaches, and from clear to turbid water.

Xenophoridae.

Xenophora conchyliophora (BORN 1780) (55) is well camouflaged because it cements fragments of empty shells of other molluscs and stones to its own shell. Consequently, it looks like a small pile of rubble. Individuals living within the turtle grass cement gastropod and bivalve shells to their shell; individuals living on gravel cement small pebbles into their shell which may become quite heavy as a result. *Xenophora* feeds on unicellular and filamentous algae growing on soft sediment, gravel and sea grass, in 2-6 m depth. It moves in leaps, similar to *Strombus.* The sicle-shaped operculum is used as brace in the substrate against which the animal pushes with its foot in order to leap foreward. Snails turned upside down by a fish or crab can right themselves rapidly by twisting the foot around the shell, anchoring the operculum in the sediment and, with a pull of the foot, return to the normal position.

Strombidae.

The four species of *Strombus* (56-58) prefer to live in turtle grass meadows. They feed on unicellular and filamentous algae on soft and hard substrates. Juveniles of both *Strombus raninus* GMELIN 1791 (57) and *Strombus pugilis* LINNÉ 1758 (56) creep through algal tufts and mosses covering rocks in search for food. They are well camouflaged there because their own shells are covered by similar algal growths. *Strombus raninus* when older and after the characteristic outer lip has been secreted, changes its mode of locomotion to the characteristic leaping type, and its environment from hard to soft substrates. In general, adult individuals of *Strombus* move by anchoring the pointed, sicle-like solid operculum within the sediment. Then, with a powerful push of the foot, the animal is lifted from the sediment and pushed foreward. The operculum is then pulled free from the bottom and anchored in a new, more foreward position, for a new push of the foot. Adult *S. raninus* prefer very shallow turtle grass meadows, where they may form large populations. They are very common in the shallow lagoons behind the reefs of Ensenada Chengue, Nenguange and Cinto. Depending on the hardness of the substrate in these lagoons, the adults when resting may bury themselves entirely except for the most anterior portion of the shell, or may remain on the surface. In the latter case the shells are strongly overgrown by sessile organisms.

Strombus pugilis avoids hard bottoms and lives in 1-5 m depth on sandy and muddy bottoms among turtle grass. Often an area noted for large populations seems to be without a single individual. This is because all individuals of a population may rest completely burried in the sand one time and at other times be moving about and feeding. *Strombus costatus* GMELIN 1791 is rarer than the other three species, and most adults have a very heavy, thick-walled shell. It prefers an environment similar to that of *Strombus gigas* (LINNÉ 1758) (58). Juveniles of the latter species have a thin fragile outer lip and prefer very shallow lagoonal areas with soft substrate and dense turtle grass in which they can hide. Here they often co-occur with the juveniles of *Strombus pugilis.* Older individuals of *S. gigas*, with flaring and solid outer lip, move to deeper waters and prefer sea-grass bottoms in 1.5-5 m depth. Where the snails are not collected for human food or for shell hunting, large populations of this large gastropod may be present. Old shells of *S. gigas* are commonly strongly encrusted with all types of sessile organisms, including, for both *S. costatus* and *S. gigas*, heavy corals. Where the bottom is soft old individuals still bury themselves totally in the sand when resting. Here the outside of the shell slowly becomes corroded. In very old individuals of *S. gigas*, and perhaps also *S. costatus*, the shell has become thickened from within and corroded from the outside resulting in a small and very heavy individual, which is known as *Strombus samba* and was encountered rarely in Cañaveral, Cinto and Nenguange. Adult individuals of both species usually stay away from the surf, but when spawning they move into the breaker zone and deposite their egg masses of up to halve-a-million eggs within the oxygen rich water just below tide line (BANDEL 1976).

Cypraeacea.

Trivia pediculus (LINNÉ 1758) (59) usually covers most of its outer shell with its opaque brownish mantle decorated by red spots, white lines and a greenish fluorescent hue. In 0.3 to 2 m depth, *Trivia* searches for tunicates encrusting the lower side of stones and rock surfaces in shaded crevices and overhangs and between reef corals and their debris. Members of the genus *Cypraea* also keep their shell generally hidden below a mantle with a completely different colour and ornamentation than is seen on the shell itself. Only two species are regularly found — the large rare *Cypraea zebra* LINNÉ 1758 (60) and the middle sized more common *Cypraea cinerea* GMELIN 1791. Both species live in 0.5 to more than 5 m depth below stones and coral debris of cliffs and reefs. They feed on crust-forming colonial animals which they graze or bite off from hard substrates. Rarely a third species, *C. spurca acicularis* GMELIN 1791 is associated with *C. cinerea.*

Simnia acicularis (LAMARCK 1810) (61) and *Cyphoma gibbosum* (LINNÉ 1758) (62) live on gorgonarian seafans. The small spindle-shaped *Simnia* feeds on the single polyps of *Gorgonia,* whereas the larger cowrie — like *Cyphoma* scrapes off polyps together with their spicular calcareous skeleton from the central black organic rod. At least two individuals of either species alone or together are usually found on a single seafan. *Simnia* and *Cyphoma* occur wherever seafans grow in 0.5 to about 10 m depth. In both species the shell is covered under muscular mantle. The extensive mantle can be completely withdrawn into the shell when the animals are attacked or disturbed. They move away from their feeding place like a mountain climber attached to the rope of a long mucus rod that they produce with their foot.

Naticacea.

The Naticidae (63-66) do not only rest but also move within the sediment. During motion they cover much of their glossy shell with the frontal and lateral foot-lobes. When disturbed the body is retracted completely and the horny or calcareous operculum can seal the aperture tightly. Naticids from the vicinity of Santa Marta feed on bivalves, gastropods and scaphopods living within the sediment. Prey is hunted within the sediment and enveloped by the foot. In this position a round hole is drilled through the shell and, with the help of a long proboscis, the soft tissue is extracted. *Polinices lacteus* (GUILDING 1834) (63) lives in fine sand to fine gravel from the intertidal zone to about 2 m depth. *Polinices hepaticus* (RÖDING 1798) prefers medium to fine sand from 0.5 to more than 10 m depth. *Natica canrena* (LINNÉ 1758) (65), which is larger, prefers coarse clean sand from the intertidal zone to more than 10 m depth. *Natica marochiensis* (GMELIN 1791) prefers fine-grained sediment and muds in more than 3 m depth and may also tolerate slightly brackish water. In the delta of the Rio Magdalena it commonly occurs in shallower depth within muddy estuarine areas. *Natica livida* (PFEIFFER 1840) (66), which is smaller, is the most common naticid in the area and is found in practically all fully marine sandy and muddy substrates in 1-5 m depth. *Sinum perspectivum* (SAY 1831) (64) is more common in greater depth but single individuals may be found in coarse sand below 3 m depth. The presence of naticids hidden within the sediment is most conspicuously indicated by their circular sand-collar egg capsules scattered about on the surface of the sea bottom (BANDEL 1976).

Tonnacea.

The tonnaceans (67-74) are represented by a number of carnivorous species with medium- to large-sized shells of diverse shape. *Cypraecassis testiculus* (LINNÉ 1758) (69), with an oblong heavy shell, also lives in the coral reef lagoon. It hides during the day in coarse grained calcareous sand, but hunts echinoderms, especially burrowing irregular seaurchins, at night. It drills through the thin calcareous corona of the sea urchin with the aid of acid glands in the proboscis. *Phalium granulatum* (BORN 1778) (67) has a similar mode of life but lives outside of the lagoons on sandy bottom among sea grass and at greater depths. *Cassis madagascariensis* (LAMARCK 1822) (68) and *Cassis tuberosa* (LINNÉ 1758) have large, solid and heavy shells. They feed in the same manner as *Cypraecassis* by drilling holes into the coronas of sea urchins and sanddollars with the aid of acid secretion from the tip of their proboscis. The corona of regular sea urchins is penetrated by only one hole, at a random location; sanddollars may be pierced by many holes in order to reach most of the soft tissue between the pillars supporting the flat corona. Juvenile individuals of *Cassis* bury themselves in the sand when resting, but the large adult individuals commonly have become to large and heavy to be able to hide completely in the sediment. The uppermost portion of these shells, therefore, is densely covered by sessile organisms. Both species of *Cassis* seem to prefer the same kind of food and live in about the same environment, but *C. madagascariensis* prefers water deeper than 3 m and *C. tuberosa* may follow sanddollar populations up to just below the intertidal zone of sandy beaches.

Charonia variegata (LAMARCK 1816) (74), the "triton trumpet", is a large carnivorous gastropod. It feeds on holothurians, star fish and sea urchins. A feeding *Charonia* may leave a trail of empty coronas of rock-dwelling sea urchins. The soft tissue of the sea urchin is reached through a hole drilled into the leathery epidermis connecting teeth (laterna aristoteles) with corona. Holothurians and star fish are swallowed whole and their skeletal remains reappear in the *Charonia* feaces (BANDEL 1974). *Charonia* rarely lives on rocky substrates in shallow water, and individuals living there usually are much smaller than those that roam the sea gras flats of about 5 m depth.

Species of *Cymatium* (71-71) and *Bursa* (73) prey on worms, barnacles and molluscs. *Cymatium nicobaricum* (RÖDING 1798) (71) lives in shallow water of calm bays and coral reef lagoons, resting and hiding under rocks when not searching for prey. *Cymatium muricinum* (RÖDING 1798) (72) is less common than *C. nicobaricum.* It prefers hard substrates in calm shallow water with a generally muddy bottom; slightly brackish and hypersalinal lagoon conditions are tolerated. *Cymatium pileare* (LINNÉ 1758) and *Bursa granularis cubaniana* (ORBIGNY 1842)

(73) often are found living together in 0.2 to 3 m depth. They prefer a rocky environment with clear water and strong currents and are commonly found where corals grow on rocks and cliffs or within the coral reef. Other species of the genus *Cymatium* like *C. krebsii* (MÖRCH 1877), *C. vespaceum* (LAMARCK 1822), *C. moritinctum caribbaeum* CLENCH & TURNER 1957 and *C. parthenopeum* (VON SALIS 1793) are rarely associated with the more common species. In the coral reef *Bursa thomae* (ORBIGNY 1842) is infrequently found.

Tonna galea (LINNÉ 1758) (70) with its large, almost spherical shell lives on well sorted rippeled, unconsolidated sand bottoms at depths greater than 5 m. Even large adult animals bury themselves completely in the sand and lie hidden when resting. *Tonna* feeds mainly on holothurians which, even when rather large, are swallowed whole in a long lasting feeding process.

Neogastropoda.

The radulae of most species of neogastropods mentioned here have been illustrated and described by BANDEL (1984).

Muricidae.

Murex pomum GMELIN 1791 (76) prefers subtidal sandy and muddy substrates below wave action. It rarely is found in rock-covered areas or on hard substrates where *Murex brevifrons* LAMARCK 1822 (77) lives. *M. pomum* rests hidden within the sediment and preys on molluscs living within the soft substrates. Thin shelled bivalves, the most common prey, are excavated and then opened by breaking the margins of the valves by forcing the foot between the valves or by drilling a hole at the valve margin where the shells are thinnest. The long, very extensible proboscis is inserted through the hole and the soft tissue is extracted. *Murex pomum* may also overcome very active individuals of *Strombus pugilis* of the same size as itself in spite of strong opposition by powerful strokes of the foot armed with the pointed operculum. *M. brevifrons*, in contrast, preys mainly on bivalves, especially those with very solid and thick shells. It drills a hole through the valves of large oysters and the even thicker shells of *Spondylus*, and will penetrate the thickest parts of *Pinna* or *Atrina* shells. The proboscis is then extended into the prey to feed on the soft tissue. *M. brevifrons* does not bury itself in the sediment, and the shell is strongly encrusted. *Murex recurvirostris* (BRODERIP 1833) (75) lives on fine sand, on muddy bottom from 1.5 m to greater than 10 m depth. It feeds mainly on bivalve species that live buried deeply within the sediment and on carion, especially of fish and crab. The presence of *M. recurvirostris* is only detected when the snail is seeking prey; while at rest and usually also when drilling and feeding on a bivalve, it is hidden within the sediment. *M. recurvirostris rubidus* F. C. BAKER 1897 lives in shallower water, whereas *M. recurvirostris woodringi* CLENCH and FARFANTE, 1945 prefers deeper water and here grows to large size. Shell growth in all three species of *Murex* is periodical. When a new varice is added, the animal hides in the sediment or under a rock and reappears when the varice is finished and shell thickened. Growth only occurs when the animal is well fed and it takes up to a week of non feeding time.

Morula nodulosa (C. B. Adams 1845) and *Ocenebra rosea* (Reeve 1856) (79) are small muricids that live on hard substrates and prey on bivalves by drilling a hole in one of their valves. *Morula* is found between normal low tide and about 2 m depth. Individuals living exposed to the sun on the surface of cliffs and boulders usually have a shell strongly encrusted with calcareous algae, while those found close by on the underside of rocks are free of incrustations. On exposed rocky cliffs, *Morula* forms extensive populations and preys mainly on byssally attached bivalves and perhaps also on tube-living worms. *Ocenebra rosea* prefers rocks and rocky shores from about 2 m to greater than 6 m depth. Its shell is commonly encrusted with red sponges. At about 2 m depth, *Morula* and *Ocenebra* may occur together.

The three species of *Thais* (81-83) are medium to large sized gastropods with solid shells. Adults of *Thais deltoidea* (Lamarck 1822) (82) may have a very heavy shell strongly encrusted with clacareous algae. Often much of the shell lumen is no longer used by the animal itself but is sealed off and provides living space for rock-boring bivalves. Up to two such endolithic bivalves were observed within the shell of a snail. *T. deltoidea* occurs quite commonly from normal low water to about 1.5 m depth, mainly where cliffs are continuously washed by surf. Its food consists of chitons, limpet-like gastropods and other gastropods that are mainly slow moving or sessile, herbivorous or filter feeding types. Most of its victims adhere strongly to the substrate and are pulled from it by the snail with the force of its muscular foot, aided by secretions of narcotizing liquid.

Thais haemastoma (Linné 1758) (81) is found in a wide variety of shore environments with a different shell shape in each. On rocks and concrete in muddy and sandy bays and beaches, mostly small and somewhat smooth shells are encountered. On the rocky shore, medium sized shells with nodules as decoration are found. Cliffs with populations of large sized barnacles provide the substrate for largest individuals with strong nodules decorating their shells. Gravel beaches are avoided by *T. haemastoma* and its place is taken by *Thais rustica* (Lamarck 1822) (83). Individuals of this species also live on submerged tree logs and dead submerged seafans that had been torn from their holdfasts by storms and drifted to the shore. *T. rustica* occurs on wooden pilings in all types of littoral environments. *T. haemastoma* and *T. rustica* feed on barnacles, bivalves and gastropods. The hard shell of their victims is mechanically opened by breaking and chipping, and the prey is than enveloped by the foot and bathed in digestive secretions. The softened tissue of the prey is sucked and eaten from the shell with the extended proboscis, aided by bites of the radula.

The shells of adult *Purpura patula* (Linné 1758) (80) have a very wide aperture so that they are practically limpet-like in shape. With its large shallow wide shell, *Purpura* lives above the area submerged by each wave. It is feeding on chitons and other gastropods in the splash and spray zone. To pluck its prey from the rock, to which they are able to strongly adhere, *Purpura* paralyzes them with a secretion (this secretion will stain the skin or cloth purple). The detached prey is held by the foot when eaten. The secretion may be held in the shelter of the large foot that covers all or part of the prey. In the splash zone it is not so easily diluted as it could be in the wave-swept zone just below and it rapidly palalyzes the prey. The uppermost limit of *Purpura patula* occurrence and predation marks the lower boundary of the very dense population of *Nodilittorina ziczac*.

Ocenebra sp. (127) is a small muricid that forms large populations on muddy, sandy and gravel bottoms in 0.2 to 10 m depth. It feeds on small bivalves boring a hole into one of their valves. *Aspella paupercula* (C. B. ADAMS 1850), the very similar *Aspella anceps* (LAMARCK 1822), *Favartia alveata* (KIENER 1842) and *Favartia cellulosa* (CONRAD 1848) form a group of somewhat similar muricids that often occur together but always in small numbers under rocks in 0.2-2 m depth on beaches with moderate wave action. They live only on hard substrates and prey on small bivalves primarily of the genus *Isognomon* by drilling a tiny hole through one of the valves.

Magilidae.

Representatives of the genus *Coralliophila* (84-86) are parasites on different coelenterates. *Coralliophila caribbaea* ABBOTT 1958 (85) is a parasite on seafans. Individuals of all size occur on the base of practical each *Gorgonia.* Although smaller individuals may actively crawl on the fan, larger individuals usually have become secundarily sessile attached permanently to the root system of the sea fan, where they have become encrusted by the *Gorgonia* colony itself or by sponges or tunicates. *Coralliophila abbreviata* (LAMARCK 1816) (86) and *Coralliophila aberrans* (C. B. ADAMS 1850) (84) are not fixed permanently in their position on the edge of a coral polypar but they do not usually move away from their once chosen location. *C. abbreviata* is found on colonial corals throughout the reefs and wherever corals grow. *C. aberrans* was found only where corals grew in the shelter of large slabs of rock in 1-1.5 m depth on beaches with clear water and strong wave action.

Columbellidae.

The Columbellidae (87-96) is an omnipresent group of fairly small and very active neogastropods found in practically all sublittoral marine environments. *Columbella mercatoria* (LINNÉ 1758) (91) lives on *Sargassum* weed that is attached to rocks isolated on a sandy beach. Here, in 0.2 to 0.5 m depth, it tolerates fairly turbid water and moderate wave action. *Columbella* is also present in clear water behind coral reefs, where the snails are under stones within the turtle grass meadows and in the debris behind reefs. *Columbella* is omnivorous and feeds on algae, on small animals such as hydroids, and small molluscs and on carrion. *Anachis obesa* (C. B. ADAMS 1845) (87) is found under rocks in shallow water and on turtle grass or algae on a sandy substrate in 3-5 m depth. It feeds mainly on hydroids. *Anachis sparsa* (REEVE 1859) (90) and *Anachis brasiliana* (VAN MARTENS 1897) (88) are found on the underside of rocks in 0.5-1.5 m depth. *A. sparsa,* but not *A. brasiliana,* also occurs among *Sargassum.* In the turtle grass lagoon *A. sparsa* and *A. brasiliana* are replaced by *Anachis pulchella* (BLAINVILLE 1829) (89). All three species of *Anachis* feed on small animals and carion.

Nitidella nitida (LAMARCK 1822) (92) has a very glossy shell and lives at about 0.5 m depth, always clearly below the low water line. During daylight individuals cluster in large groups, on the sandy undersides of rocks, but with darkness they hunt for small animals living among the algal tufts of the rocks or pebble strewn beaches. *Nititella nitida* is also common within *Sargassum* in this environment, but

Nitidella laevigata (LINNÉ 1758) (93) is the most common columbellids on *Sargassum*. It is totally herbivorous and utilizes almost the whole plant rejecting only stems and larger veins. *Mitrella ocellata* (GMELIN 1791) (94) lives under rocks in the zone just above that of *Nitidella nitida*. Both *N. nitida* and *M. ocellata* migrate up and down with the tides; *M. ocellata* occurs between tidal line and about 0.5 m depth; *N. nitida* at 0.5 m depth. *Mitrella argus* (ORBIGNY 1842) (95) is found most commonly on *Sargassum* together with *N. laevigata*, but in contrast to the later, it feeds on small animals it finds on the *Sargassum* rather than on the plant itself. *Mitrella lunata* (SAY 1826) (96) is also found on *Sargassum*, and may also occur on turtle grass.

Nassarina monilifera (SOWERBY 1844) and *Aesopus stearnsii* (TRYON 1883) are columbellids with a highly sculptured shell. *Nassarina* lives among algal tufts on rocks and reef debris in shallow water, while *Aesopus* lives in and on sand.

Buccinidae.

The buccinid neogastropods in general are larger than the columbellids, but *Engina turbinella* (KIENER 1835) is an exception. This small gastropod is found on all hard substrates at about 0.5 m depth. The shell of individuals living on the crest of coral reefs is commonly strongly encrusted with calcareous algae. *Engina* preys on small animals, most probably worms. *Pisania pusio* (LINNÉ 1758) prefers shallow water from the intertidal zone to about 2 m depth. It lives in agitated and well oxygenized water in shaded areas among debris under cliffs and within or on the sides of coral reefs. It may move about very rapidly on its narrow foot within clefts and open spaces, but on soft sediment it can move only with difficulty *Pisania auritula* (LINK 1807) (98) is omnipresent on rocks and among pebbles from the intertidal zone to 2 m depth. It searches very actively for food and is also found where water is not well oxygenated and where particles of hard substrate can only be reached by crossing soft sediment. *Pisania* feeds on worms, barnacles and small molluscs aided by a long, extensible proboscis. *Dolicholatirus cayohuesonicus* (SOWERBY 1878) and *Colubraria swifti* (TRYON 1881) are small buccinids with a morphology resembling that of turrids. They probably feed on worms living within algal mosses and tufts covering large rocks, within or just below the infralittoral fringe. Both species are common on the surface of rocks and also on the lower sides of rocks that are covered with encrusting animal colonies.

Nassariidae.

Engoniophos unicinctus (SAY 1825) (99) lives on mud to muddy sand in 1-8 m depth. In shallow water it usually co-occurs with *Nassarius vibex* (SAY 1822) (104), in deeper water with *Nassarius albus* (SAY 1826) (103). The later is also common among well sorted medium sized to coarse sand within the wave-swept intertidal zone. Members of all three species actively search for carion and appear within seconds from their hiding places within the sediment when they sense food. In addition to carion, soft bodied animals are also preyed upon. *N. vibex* also lives in areas with slightly raised or lowered salinity and can even tolerate fresh water for several hours without appearent ill effect.

Melongenidae.

The much larger *Melongena melongena* (LINNÉ 1758) (100), like *Nassarius vibex*, can tolerate deviation from the normal salinity well and, therefore, is found in estuarine areas and in hypersalinal lagoons. Its favoured food consists of thin-shelled deeply buried bivalves, mainly of the genera *Tellina* and *Tagelus* which it seeks on muddy to sandy bottom from just below low tide line to more than 10 m depth. To reach bivalves that live in deep burrows it can, itself, burrow deeply into the sediment. Small individuals of *Melongena* can burrow more deeply than larger individuals but the large individuals are able to reach deeply buried prey with a very long extensible proboscis. Most individuals of *Melongena*, except those with an extremely large shell, are completely hidden within the sediment when resting. Populations of the genera *Engoniophos, Nassarius* and *Melongena* are large within their preferred environments.

Fasciolariidae.

Fasciolaria tulipa (LINNÉ 1758) (107), in contrast, is never common. It is found throughout the littoral zone, on hard as well as soft substrates. *Fasciolaria* preys on prosobranch gastropods of all types except species of the toxoglossan genera *Conus* and *Terebra*, but prefers *Strombus*. Non-feeding individuals lie buried within the sediment if it is soft enough. *Leucozonia nassa* (GMELIN 1791) (101), also a fasciolariid gastropod, occurs primarily on cliffs and, to a lesser degree, on boulders and rocks from the base of the intertidal zone to a maximum depth of 3 m; it is most common just below the intertidal zone. The solid, large shell is usually encrusted with calcareous algae. The snail moves about slowly on the rocky cliff in search of barnacles, its favoured prey, and to a lesser degree, byssally attached bivalves. Individuals feeding on the settlements of large barnacles on cliffs exposed to the open sea grow to larger size than those feeding on smaller barnacles and bivalves on cliffs in more protected areas. Populations of both small and large individuals, however, reach maturity, copulate and spawn (BANDEL 1976).

Leucozonia ocellata (GMELIN 1791) (102) prefers the rocky intertidal substrate above the upper limit of *L. nassa*. Here it roams through the tidal and splash pools, searching the intertidal platforms primarily for byssally attached bivalves of the genera *Isognomon* and *Brachidontes* and for the attached worm-like *Petaloconchus* and other gastropods as well.

Latirus infundibulum (GMELIN 1791) (105) crawls very slowly on mud, sand and gravel substrate searching for small bivalves and carion. The bivalve prey, such as *Anomalocardia*, consists of species that live shallowly buried within the sediment. *L. infundibulum* lives from the intertidal zone to 5 m depth to greater depth in quiet environments of protected bays. It moves through the sediment surface only partly buried, so that the uppermost portion of the shell extends above the sediment and is encrusted by sessile organisms. The very similar *Latirus angulatus* (RÖDING 1798) (106), in contrast, avoids soft substrates and prefers coral-rich hard substrates at 2 to more than 6 m depth. A favorite habitat for this species is the hollow lower side of hemispherical coral colonies in backreef areas and near *Acropora* patch reefs within the deeper lagoon. It feeds primarily on tube-dwelling worms.

Olividae and Olivellidae.

The glossy shell of *Oliva reticularis* Lamarck 1810 (111) is covered almost totally by the foot when the snail moves through the sediment. *O. reticularis* lives in sandy bottoms from the surf-beaten beach to about 10 m depth. The food consists of worms, molluscs dwelling within the sand and carion. It senses food with its siphon, which can be extended to a length greater than that of the shell itself. The siphon is held above the sediment surface as *Oliva* moves towards its prey. The snail crawls onto the sediment surface only very shortly before reaching the prey or carion, envelopes the food with the foot and quickly burrows into the shelter of the sandy bottom, taking the food with it. In deeper water, in mud as well as sand, the very similar *Oliva scripta* Lamarck 1810 replaces *O. reticularis.*

The life habits of *Olivella nivea* (Gmelin 1791) (114), *Olivella perplexa* (Olson 1956) (115), *Olivella adelae* Olsson 1956 and *Olivella petiolita* (Duclos 1835) (113) are similar to those of *Oliva. Olivella nivea* prefers pure coarse grained sand, *O. perplexa,* in contrast, mud and *O. petiolita* and *O. adelae* sand. *O. adelae* may escape from predatory starfish or gastropods by swimming away: As the wing-like sides of the foot are flapped up and down, the *Olivella* is lifted into the water with foot up and shell hanging down. All species of *Olivella* prey on small bivalves and worms dwelling within the sediment, but in contrast to *Oliva,* swallow their prey in one piece. Individuals of *O. nivea* had their intestines filled with shells of *Caecum* which had been swallowed as wholes.

Mitridae.

The mitrid gastropod *Vexillum puella* (Reeve 1845) (110) lives on and under rocks in the reef and its debris in 0.5 to 2 m depth; it is especially common on the wave-swept platform of the coral reef. On cliffs with very strong wave action *V. puella* lives in crevices or holes excavated by rock-dwelling sea urchins to avoid the surf. Less common are *Vexillum hendersoni* (Dall 1927) under rocks near the reef crest and *Vexillum dermestinum* (Lamarck 1811) under rocks of rock and pebble beaches below tidal zone to 2 m depth. All species of *Vexillum* feed on worms. *Mitra nodulosa* (Gmelin 1791) lives in the lagoon of reefs and is uncommonly found below coral slabs.

Turbinellidae.

Other than *Strombus gigas, Turbinella angulata* (Lightfoot 1786) (109) is the largest gastropod in the area of Santa Marta. It roams with the heavy shell held up high on soft substrates at 1 to 10 m depth. Prey consists of endobenthic animals such as large worms and thin-shelled bivalves with a gaping upper shell end. To reach their prey *Turbinella* burrows some way into the sediment and extends a very long proboscis even further down following the tubes for exhalent or inhalent currents produced by the worm or the bivalve. Even fairly large adult individuals of *Turbinella* at rest are hidden within the sediment, and only the very largest can no longer burrow down far enough to bury the whole shell. Consequently the portion of their shell opposite the aperture extends above and is covered by sessile organisms. When buried within the sediment only the tip of the siphon extends above the sand and a small hill of sand indicates where the water of the exhalent current comes to the surface. The shells of dead individuals often serve as home for hermit crabs.

Vasidae.

Turbinella avoids hard substrates, but *Vasum muricatum* (BORN, 1778) (108) searches for food on soft mud, sand as well as on rock and reef bottom. Only very steep rock cliffs are avoided, though it is able to climb vertical cliff walls. *Vasum* occurs from 1 m to greater than 10 m depth. Its shell does not become as large as that of *Turbinella*, but if may become very thick and heavy, and may become even heavier because of encrustations including even complete coral colonies. *Vasum* moves very slowly when persuing prey, which consists largely of worms that live buried deep between rocks or within soft substrate. *Vasum*, like *Turbinella* and *Melongena*, reaches its prey with a proboscis that can be extended to several times the length of the shell. This proboscis follows the feeding of breathing tubes of the endobenthic animal until reaching the animal. Young individuals of *Vasum* can hide within the sediment and can burrow deeply, while older individuals no longer burrow in the sediment.

Volutidae.

Voluta virescens LIGHTFOOT, 1786 (121) lives on muddy and sandy bottoms below 5 m depth and probably preys on worms. During daylight the animals are hidden within the sediment and come to the surface only at night. On many shells, a single anemone is attached, which is retracted during the active phase of *Voluta* and opens when the snail is in resting position. Because the shell of the snail is buried a few centimeters deep in the sediment, the coelenterate can retract completely into the sediment when disturbed.

Marginella prunum (GMELIN 1791) (112) prefers muddy sand at greater then 0.5 m depth. It moves within the sediment searching for food consisting of various sand-living animals, but does not leave a trail visible on the surface. As it moves the shiny shell is almost completely covered by the foot. The shell of *Hyalina avena* (KIENER 1834) (116) is very similar to that of *Marginella* but much smaller. It lives in sheltered locations on rock strewn beaches with calm to moderately strong wave action, from just below the intertidal zone to about 1 m depth. In contrast to *Marginella*, *Hyalina* does not burrow in sediment but lives among algal tufts and moves through these thickets preying mainly on small bivalves. The small clams are enwrapped with the foot and remain here until their tissue has been cleaned out with the help of the proboscis and the radula.

Marginella lavalleana (ORBIGNY 1842) lives in great numbers in about the same type of environment within algal thickets covering gravel, sand and mud, during periods of clear water in 0.2 to 1.5 m depth. It has a minute pure white shell. *M. lavalleana* preys on small worms that live in large numbers in this protected algal mat environment. Here also the small *Persicula pulcherrima* (GASKOIN, 1849) with a colourful shell, is abundant on algal mats down to depths or 2 m hunting for minute animals. The larger *Persicula interruptolineata* (MÜHLFELD 1816) (117) moves in the same way as its smaller relative, but prefers well sorted coarse sand at 0.5 to 5 m depth. It leaves the sand to get some food particles, such as carion; otherwise, it hunts for prey within the sediment and feeds while it is buried. Individuals found in yellow, well sorted sand have spots of yellow, orange and brown on their large foot that covers the shell during motion. Others living in sand of the reef lagoon are spotted with green and brown.

Morum oniscus (LINNÉ 1767) lives in 0.5 to 2 m depth hidden within the open spaces between reef debris and coral fragments just behind reefs and within the reef lagoon. It has a medium sized cylindrical shell, is active at night and feeds on worms.

Conidae.

Toxoglossan neogastropods are represented by two morphological types- the cone-shaped shell of *Conus* and the slender elongated shell of *Terebra* and turrids. *Conus mus* HWASS 1792 (118) preys on worms living among rocks and on rocky surfaces from the tidal zone to about 2 m depth. It lives both in turbid water of beach rock platforms on sandy shores as well as in clear water of the coral reefs; on shores with strong wave action as well as shores with calm conditions. On wave-swept cliffs it hides in crevices and the holes dug by rock-living sea urchins to avoid the direct impact of the waves, it lives in tidal and splash pools if the water in them is continuously renewed. Only within the coral reef environment are populations of *C. mus*, which are rich in individuals, mixed with the less numerous populations of *Conus regius* GMELIN 1791 (120). The later lives near and within reefs in 1.5 to 5 m depth within well sorted calcareous sand when resting. It feeds on sand-dwelling worms. Spawning individuals of *C. regius* gather in large number on the underside of coral debris near the sandy bottom (BANDEL 1976). *Conus ermineus* BORN 1778 is rarely found with *C. regius.*

Conus jaspideus GMELIN 1791 (119) is the most common species of *Conus* in the area. It may occur in large numbers on sandy and muddy bottoms in 1 to more than 6 m depth, where it feeds on endobenthic worms. It is usually hidden within the sediment, into which it can burrow from the surface to be totally hidden in about one minute. It burries by pushing the foot into the sediment, anchoring it by expending its frontal part and then pulling the body forward by contracting the spindle muscle. This sequence is repeated at 5 to 10 second intervals. While resting in the sediment the long siphon rises above the substrate and moves back and forth testing passing water for smells. If prey is detected, the snail comes out of hiding and reaches for it by crawling on the sediment. *C. jaspideus* may also live in sligthly hypersaline shallow turbid warm lagoonal environments.

Terebridae.

Terebra taurinus LIGHTFOOT 1789 (123) is a large, slow moving gastropod with a very slender heavy shell. It is found in large populations only where subsurface fresh water appears in the bottom sediment and under calm conditions. This is the case in about 2 m depth in the bay of Taganga just below the sandy shore. Here numerous individuals crawl through the sand with only very little of their shell visible, leaving a very conspicuous trail. Its food consists of worm that lives under these very special conditions in the sediment in great abundance.

Another worm with similar requirements but living in beach sand through which fresh water flows from a small stream pooled up behind a sandy beach ridge is the main source of food for *Terebra cinerea* (BORN 1778) (122). Large populations of this species, therefore, are found in such beaches in fine to coarse sand. *T. cinerea* changes its location rapidly and escapes from predators by crawling to the surface of the sediment and extending its wing-like propodium so that it acts like a sail just when a wave washes up the shore. The current transports the snail upshore and, in the very short period of calmness before the wave can wash it downbeach, *T. cinerea* folds its propodium together and pushes it into the sand; here it expands the foot again to form an anchor so that subsequent waves will not pull the snail from its holdfast even though its shells is washed back and forth with each wave. With single rapid pulls the foot pulls the very smooth shell slowly into the sediment until the apex points vertically and gives only little resistance to wave currents. The snail burrows into a position horizontal to the beach surface in order to search for prey and to rest. To hunt *T. cinerea* moves within the sediment with most of its shell covered by the foot.

Turridae.

Several species of *Terebra* are found in different sublittoral environments, in soft substrates ranging from coarse sand to mud. Several species of turrids are also present in similar environments. *Crassispira* sp. (128), for example, is commonly found in sandy substrates from 2 to more than 9 m depth (BANDEL 1976). The small turrid, *Ithycythara lancelolata* (C. B. ADAMS 1850) (124), prefers mud to very fine sand and is a regular inhabitant of muddy bottoms seaward of the outlets of the fresh water streams in the delta of the Rio Magdalena. It also occurs in most fine-grained bottoms from 3 m depth onward. *Drillia solida* C. B. ADAMS 1830 is one of the few species of turrids that does not live within or on soft sediment, but on the underside of rocks in 0.5 to 2 m depth. It hunts for worms harpooning them with its specialized radula (BANDEL 1984). The littoral turrids encountered here most probably all feed on worms.

Pulmonata.

The pulmonate gastropods are represented primarily by two species — the high spired *Melampus coffeus* (LINNÉ 1758) (125) and the limpet-like *Siphonaria pectinata* (LINNÉ 1758) (126). *Melampus* lives within the mangrove swamps and is a characteristic animal of that habitat; it prefers brackish water. *Siphonaria* lives attached to rocks in the upper intertidal area wave-splash zones. *Melampus* usually is in large populations and feeds on the decaying leaves of the mangove above the water surface on moist and muddy ground. *Siphonaria* feeds on algal tufts and crusts covering huge granite boulders scattered on the sandy beaches as, for example, between Rodadera and Cienaga Grande and north of Cañaveral. The water may be quite turbid and the wave action moderate to strong.

Opisthobranchia.

Dead shells of a number of species of the pyramidellids are commonly found in fine grained sediments from 1 m depth onward. Most of these live on larger animals like worms and molluscs as parasites, but only one, *Cingulopsis babylonica* C. B. ADAMS 1845 was studied while alife. Several of these minute snails can be found on the shell of *Bursa* near the apertural edge close to the siphonal canal. Periodically the parasites extend their proboscis and suck liquid from the mantle edge of *Bursa*. Within the coarse ornament of the *Bursa* shell the pyramidellid finds shelter and a substrate for oviposition (BANDEL 1976).

Bulla solida (GMELIN 1791), *Bulla striata* BRUGUIERE 1792, *Haminoea elegans* (GRAY 1852) and *Haminoea antillarum* (ORBIGNY 1842) have medium to large cylindrical oval shells. As these bubble shells move about, they form a mucus tunnel with the whole surface of their mantle and foot that covers the shell during motion. These mucus tunnels become visible only when suspended material adheres to the sticky tunnel surface. *Bulla* and *Haminoea* feed on algae and prefer to live in thickets of filamentous algae irregardless whether they are on rocky surface or muddy bottom. Both genera can be found in slightly brackish lagoons as well as in calm lagoons of normal salinity. The shells of *Bulla solida* in the sandy reef lagoons of Chengue, Nenguange, Cinto and Canaveral become especially large and solid.

Hydatina vesicaria (LIGHTFOOT 1786) lives well hidden in sand among turtle grass in water deeper than 1 m and *Micromelo undatus* (BRUGUIERE 1792) is found within algal tufts covering cliffs and rocks just below the intertidal zone. Both species, which are uncommon, cover their shell with their mantle and foot while moving on top of the sediment through entangled algal growths.

Cylichnella bidentata (ORBIGNY 1841), *Atys caribaea* (ORBIGNY 1842), *Atys riiseanus* MÖRCH 1875 and *Tornatina candei* (ORBIGNY 1842) live on and in mud in lagoons from the intertidal zone to several meters depth. Living individuals are common only periodically during the year.

Aglaja evelinae (MARCUS 1955) is common under rocks in 0.2 to 1 m depth; is less common on *Sargassum*. This alga is the normal habitat of *Elysia ornata* (SWAINSON 1840). Because of its brown colour, it is well hidden in the brown *Sargassum*. Individuals of this species are able to swim, most probably only as an escape reaction, by bending sideways near their centre and moving head and end of foot towards each other at one side and rapidly on the other side and thus ascending from their holdfast with a ziczac motion. *Elysia* sheds long, solid, spirally twisted feaces about 5 mm wide and 3 cm long. The consistence of the feaces indicates that this sea slug lives on algal crusts and filaments growing on the *Sargassum*, or perhaps on the *Sargassum* itself.

A rarer inhabitant of Sargassum is *Scyllae pelagica* (LINNÉ 1758). It is found on *Sargassum* both attached to rocks in the intertidal zone and drifting in the open sea. *Scyllae* is up to 2.5 cm long and is similar in colour to *Sargassum*. Its escape movements and swimming motions are like those of *Elysia*. The animal moves from one frond to another by staying attached with the extreme end of its foot until the frontal portion of the foot firmely graspes the new frond. Feaces are composed of an inner organic rod surrounded by an unequally thick layer containing detrital particles. The round rod is about 0.2 mm wide and up to 2 mm long and indicates that its producer feeds on algal material growing on the *Sargassum* weed.

Another, common inhabitant of *Sargassum* is *Stylocheilus longicauda* (Quoy & Gaimard 1824), which grows to a length of about 4 cm. It lives like *Scyllae* and *Elysia*, and it also is well camouflaged among the *Sargassum* with an enlongate brown, filament-bearing body. *Phyllaplysia engeli* Marcus, 1955 is the fourth opisthobranch gastropod found regularly on *Sargassum*. It is a flattened sea hare up to 1 cm long that is brown when living on *Sargassum*, but green when dwelling on turtle grass. On the green turtle grass, even the shells of the veligers developing within the colourless egg masses and the newly settles slugs are green (Bandel 1976). Feacal rods of this species are round spirals, 0.2 mm wide. Their consistence indicates that the food eaten is algae growing on the living substrate.

Tridachia crispata (Mörch 1863) is very common feeding on algal tufts, especially those covering hard grounds in coral reef lagoons, but also below rocky beaches down to depths of 2 m. The up to 45 mm long *Tridachia* is most abundant during summer and fall when the water is very clean. The local population increases rapidly in individuals because from the egg masses miniature adults hatch, leaving the larval shell behind. This is also the time when the algal mats and thickets on muddy and sandy bottom in calm bays such as Taganga and Santa Marta provide abundant food for the large sea hares *Aplysia brasiliana* (Rang 1828) and *Aplysia cervina* (Dall & Simpson 1901) which are up to 7 cm long. *Dolabrifera dolabrifera* (Rang 1828) and *Bursatella leachii pleii* (Rang 1828) which are up to 6 cm long, live together with the *Aplysia*. During the rainy season, when the algal growths disappear, *Aplysia, Dolabrifera* and *Bursatella* only survive elsewhere, under rocks in the infralittoral fringe of calm beaches and under rocks and algal-covered hard substrates within lagoons. *Aplysia* has two lateral skin-flaps that can be used for swimming. The rapidly growing sea hares (*Aplysia*), and ragged sea hares (*Bursatella*) and sea cats (*Dolabrifera*) feed mainly on filamentous algae and other green algae and grow rapidly. At the end of the growth period of the algal mats, before the rainy season starts, the sea hares and sea cats have become fully grown and mature and it is at this time that many individuals of *Aplysia* are seen swimming towards the beaches. Here they congregate, copulate and spawn. Many individuals of *Aplysia* together form large balls of spawn usually attached to seagrass in shallow water close to the beach. The large fleshy sea hares and sea cats, after spawning, are often washed up on the beach and die.

Berthellina quadridens (Mörch 1863) and *Berthella agassizii* (Mac Farland 1909) are very similar to each other in shape and live on the underside of rocks and coral debis in 1-3 m depth. *Berthellina*, which is larger, is brightly red or orange; *Berthella* is grey. *Pleurobranchus testudinarius* (Cantraine 1840) is flattened, oval in outline, and measures up to 8 cm in length: *Chromodoris neona* Marcus 1955 and *Chromodoris perola* Marcus 1976 are a little over 1 cm long; *Peltodoris hummelincki igla* Marcus 1967 is up to 7 cm long; *Taringa telopia* Marcus 1955 is only 6 cm in length and *Dendrodoris krebsii* (Mörch 1863) is up to 2.5 cm long. All these shield-like dorids occur under rocks from about 0.5 to 3 m depth, in environments ranging from coral reef with clear water to sand and mud bottom with turbid water. Judging from the consistency of the feaces, which are fragile and organic-rich it seems probable that most dorid sea slugs feed on animals living on the rocky surfaces rather than on plant material.

Spurilla neapolitana (Delle Chiaje 1823) and *Phidiana lynceus* Bergh 1867 feed on sea anemones and are found wherever sea anemones occur. Individuals of both these colourful species will also attack fairly large anemones and suck tissue through their stalk until they die. The beautifully coloured *Flabellina engeli* MARCUS, 1968 is up to 1 cm long. It is common in about 1 m depth on soft bottom hunting soft coelenterates. *Dondice occidentalis* (ENGEL 1925) and *Favorinus auritulus* MARCUS 1955 move about and look for similar food. The minute *Calmella bandeli* MARCUS 1976 feeds on hydroids attached to rocks in the infralittoral zone. All aeolid nudibranchs from the area of Santa Marta subsist on coelenterates.

Polyplacophora.

The chitons of the area of Santa Marta have been described and illustrated by GÖTTING (1973), and most species mentioned here have been treated in this study.

The most conspicuous chitons are the large *Acanthopleura granulata* (GMELIN 1791) (2), *Chiton tuberculatus* (LINNÉ 1758) and *Chiton marmoratus* GMELIN 1791 (1). *Acanthopleura* lives on cliffs and large boulders in the uppermost intertidal and the lowermost supratidal zone where the rocky substrate is continuously moistened by spray. Below it, in the intertidal zone where rocks are continuously kept wet by the waves, both *Chiton marmoratus* and *C. tuberculatus* are found, usually together. Outside of the cliff environment, *C. tuberculatus* can also be encountered on the reef crest and under rocks within the lower tidal zone and the infralittoral fringe. All three large sized chitons feed on algal crusts, but while *Acanthopleura* and *C. marmoratus* scrape both calcareous algal crusts and non calcareous algae from the rocky substrate, *C. tuberculatus* feeds only on non-skeletal algae.

Ischnochiton pectinatus (SOWERBY 1840), *Ischnochiton striolatus* (GRAY 1828) and *Stenoplax* (= *Ischnochiton*) *limaciformis* (SOWERBY 1832) are found on the underside of rocks and coral debris in the reef area as well as in the open sea grass lagoon and on pebble and rock beaches with moderate wave action. *Stenoplax limaciformis* with a very variably dyed shell is the most common of these three species. It can tolerate being covered with a few mm of sand on its place of rest and attachment. All three species feed by scraping algal crusts from rocky substrates. *I. pectinatus* and *S. limaciformis* eat calcareous algae and *I. striolatus* feeds on non skeletal algae.

Ceratozona squalida (C. B. ADAMS 1845), a middle sized chiton that hides among barnacles or in small depressions on cliff rocks just within the low tide line or just below it is sessile to semisessile. How they feed is not known, but they do not seem to move about much. Individuals merge with their environment because their shell is covered by the same type of green algae that cover the surrounding substrate. *Acanthochitona pygmaea* (PILSBRY 1893) and *Acanthochitona spiculosa* (REEVE 1847) are found under rocks in the infralittoral zone between 0.5 and 2 m depth. The much more common *A. spiculosa* is up to 4.5 cm long and feeds on crust forming organisms like tunicates. *Lepidochitona liozonis* (DALL & SIMPSON 1901) was found only with a few individuals under rocks in 1 m depth.

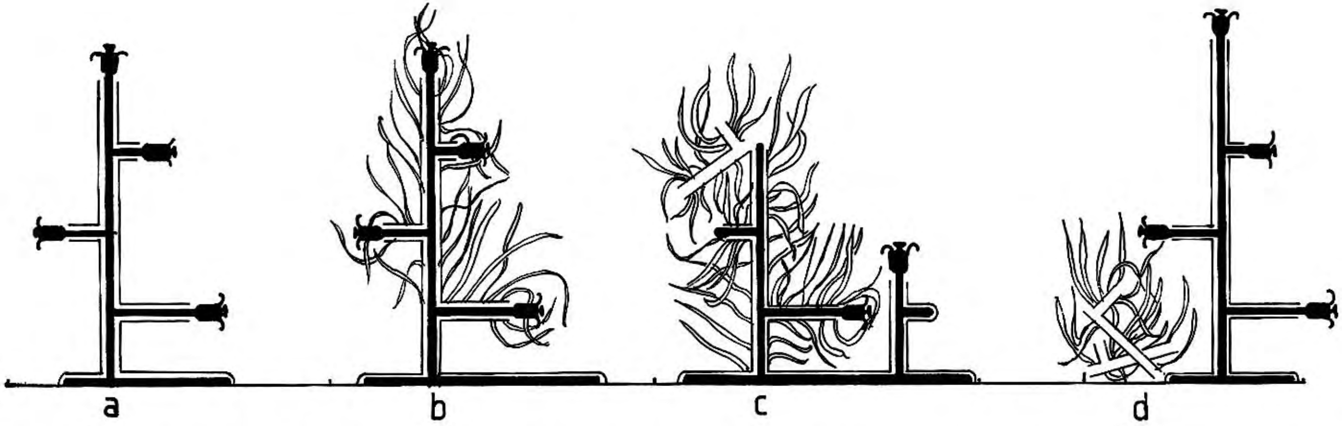


Fig. 2. A hydroid (a) with increasing overgrowth of algae (b) reestablishes itself nearby (c) and avoids being settled (d).

Abb. 2. Eine Hydroidenkolonie (a) kann der Besiedlung durch Algen (b) dadurch entgehen, daß sie in die Nachbarschaft ausweicht (c) und damit der Besiedlung die Grundlage entzieht (d).

Hydroids of the Littoral Zone.

Ecological studies based on hydroids from the littoral region of the Caribbean Sea are rare, and the situation is not much different in other parts of the world. Hydroid zonation is not well known, apart from studies carried out by RIEDL (1959, 1966), MERGNER (1969, 1977), SVOBODA (1979) and WEDLER (1975). The interrelations between hydroids and their substrates were analysed by NISHIRA (1966, 1968, 1969) and STEPHARD & WATSON (1970). The ecology of the species of estuarine hydroids has been studied in greater detail (KINNE 1955, 1956, WEDLER 1973, CALDER 1976) than that of littoral marine species. Data on the distribution, shape, size, activity and reproduction phases of littoral marine hydroids are scarce. The connection of genetically fixed shapes and ecological variability is still unknown for many species. The present account can only provide a base for further research into the matter.

The age of colony forming coelenterates is usually quite extended. For example colonies formed by several large species exist for a long time; periods of up to 18 years have been registered. However there are also short lived species, usually smaller forms such as in the Zancleidae and Campanulariidae, that have often specialized in short lived substrates like algae.

Sessile coelenterate colonies are good indicators of bathymetry. Many species prefer to live only in a certain area and individuals are usually found only within this range. Here individuals show some flexibility regarding shape and orientation of their colonies. When abiotic factors (light, water movement) change, the colonial organism can withdraw from marginal portions of its colony and reestablish itself nearby. Fig. 2 shows such a case of a colony of a *Eudendrium carneum* living in the marginal zone of the range of the species. In this case, light is the limiting factor and also competition from Chlorophyceae such as *Enteromorpha lingulata.* The hydroid can survive the attack of the epiyhyte. The colony without algal growth (a) reacts to an increase of sunlight (b) by withdrawing its coenosarc (soft body) from the infested portions of the colony and producing a new branch besides the old one (c). The empty perisarc (tube-like organic skeleton) collapses due to the algal growth on it (d), the hydroid is then free of the algal epiphyte. It can thus migrate away from an area where the competion for space by algae is increased. In the case of *Halocordyle disticha* this process of withdrawal from the old branch to a new one formed nearby is completed within two days. The whole process may be a continuous one in marginal portions of a range of a species (TARDENT 1969; WEDLER 1975). When the opposite condition results in a reduction of algal growth the coelenterate immediately regains fromerly lost territory.

Morphology and size of colonial coelenterates are influenced mainly by external factors. The most important of these are water movement and light-exposition. The size of the colony, as a general rule, increases with depth, individuals become more delicate, and colonies move further apart. Water movement determines the outline and shape of the colony as is shown in the case of *Cnidoscyphus marginatus* in Fig. 3. Characteristic colony shapes are found from the rocky cliff to deep water and on the artificial construction of the harbour jetty. Three-dimensional colony-shapes are developed in turbulent zones (a, b, h). Two-dimensional colonies grow in the area of oscillating and unidirectional currents (c, d, e, f, j, k). Colonies are arranged vertically to the current directions. When currents change and swing in the area of

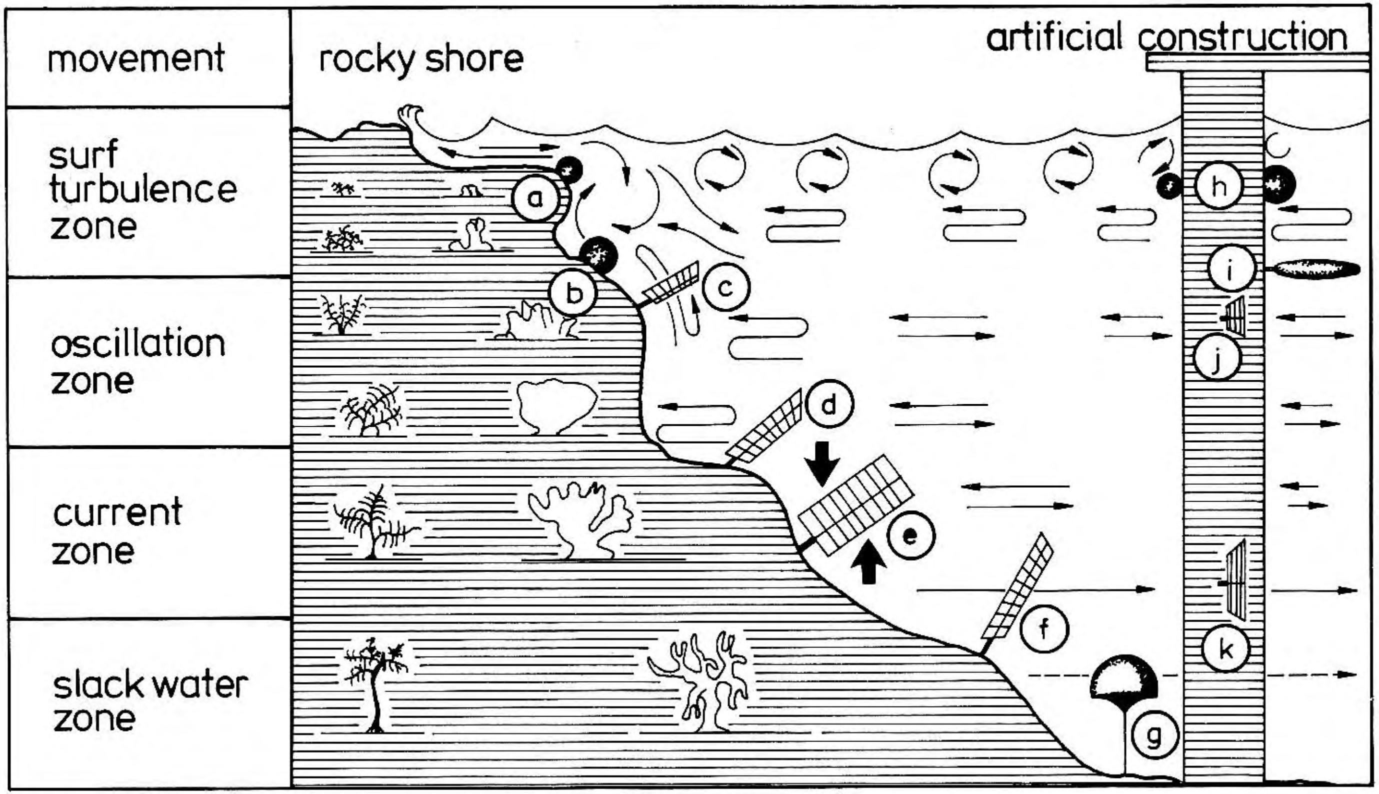


Fig. 3. The morphology of hydroid colonies depends on external factors, mainly light and currents.

Abb. 3. Die Morphologie von Hydroiden-Kolonien wird von den Strömungs- und Lichtbedingungen mitbestimmt.

the colony in a protected area, a longitudinal three dimensional shape results (i). Tree-like colonies form at places in which currents no longer influence the morphology of the individuals, in deeper water (g).

In the turbulent zone colonies are small and compact. In directed current regimes colonies grow oriented in such a way that their largest surface is vertical to current direction. Colonies usually are of bilaterally flattened shape and react to decreasing current intensity by changing to a more spherical shape. However their fabric, in contrast to that of colonies in turbulent conditions, is more delicate and they themselves are larger.

The upper sublittoral zone can be divided into subzones by the type of wave motion found there (RIEDL 1964), and its influence on the specific composition of shape, size and arrangement of sessile organisms. Of the coelenterates hydroids and goronians can be used for further characterizations of the zone of the sublittoral fringe and below (MERGNER 1977; WEDLER 1975). Species and phaenotypes can help

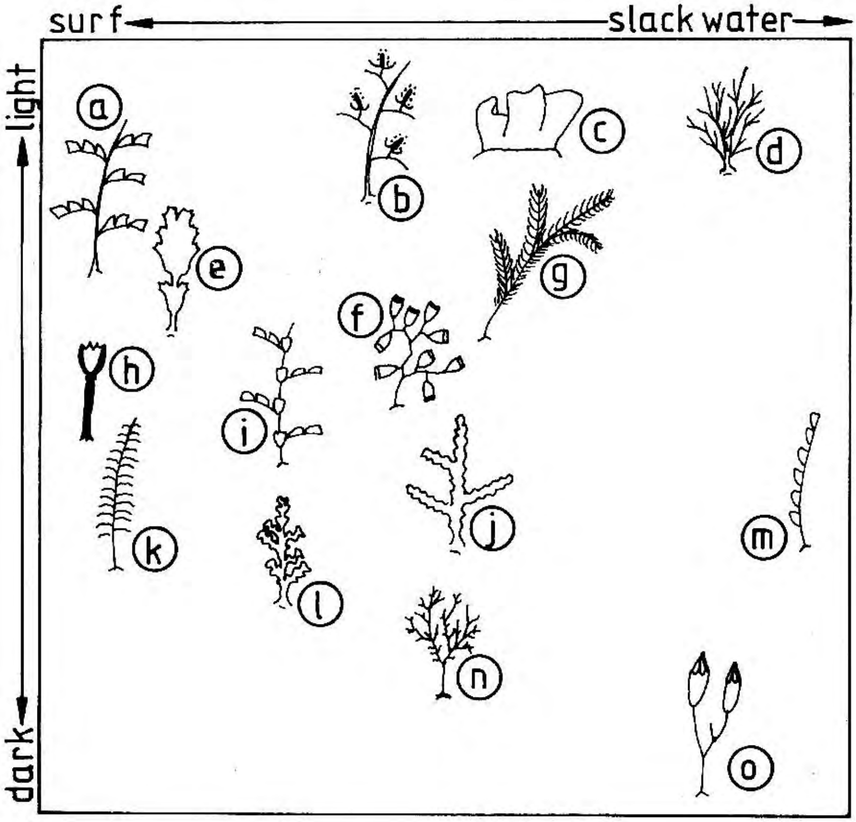


Fig. 4. Species dependence on light and currents. — Species names a-o see text.

Abb. 4. Artenspektrum in Abhängigkeit von Licht und Strömung.

to define hydrodynamic conditions much better than vagile organisms, such as gastropods and chitons. Hydroids are widely distributed and commonly found in all environments below the central eulittoral zone. There are numerous species with a wide range of adaptations to their specific living place and there are others with very specific requirements. Fig. 4 shows the preferred place within the littoral zones in relation to light (depth) and motion of the water of some hydroids: a) *Aglaophenia latecarinata;* b) *Halocordyle disticha;* c) *Millepora complatata;* d) *Halecium bermudense;* e) *Dynamena quadridentata;* f) *Cnidocyphus marginatus;* g) *Lytocarpus philippinus;* h) *Capanularia lennoxensis;* i) *Halopteris diaphana;* j) *Sertularella speciosa;* k) *Plumularia setacea;* l) *Sertularia inflata;* m) *Antennella gracilis;* n) *Eudendrium carneum;* o) *Lovenella gracilis.*

The amount of sessile organisms, as a general rule, decreases with depth. This statement is also valid for hydroids. With decreasing density of growth the ideal morphology of a colonial coelenterate can be obtained. With increased density colonies tend to become more slender. The composition of the substrate is of very little importance to the zonation of hydroids. Exceptions are substrates produced by living organisms since they themselves react to ecological changes, as is evident when algae or mobile invertebrates are considered. Some colonial coelenterates show great changes of shape at different stages of their ontogeny and activity. This is the case in species that have to deal with extreme changes as occur, for example, in estuarine areas with their changing salinities.

Hydroids that can be used as indicators for specific ecological zones will be briefly introduced. The account excludes species without apparent pattern. Two groups of species can be distinguished: 1. species living under very specific conditions of light and water movement (Fig. 4); 2. species of a wider range of habitats and reflecting the type of water movements prevailing in their morphology (for example Fig. 3).

Different species of the Milleporidae depend on the intensity of light, because *Millepora* lives in symbiosis with algae (zoooxanthellae). *Millepora* grows in protected areas, preferably bays and lagoons with constant but calm water currents. Zonation differs between environments with very clear and less clear water because bathymetrical distribution of species depends on the penetration of light into the water column.

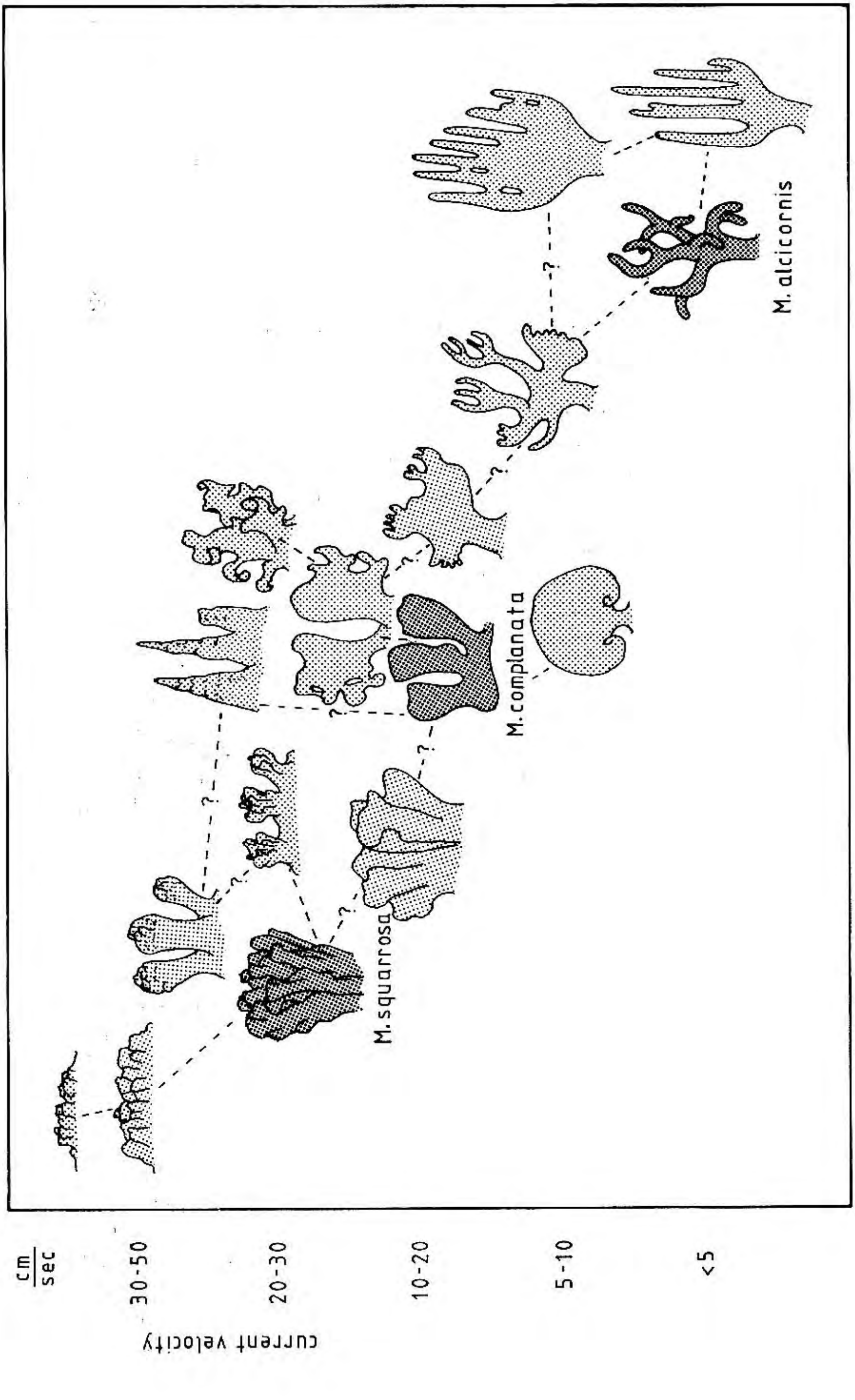
In general *Millepora squarrosa* forms regular to irregular nodular colonies on the rocky littoral as well as in sea grass flats in up to a little more than 1 m depth. Close to the water surface colonies are compacter than they are away from it. Crust-like colonies are found on rocks as well as on the roots of mangrove trees. *Millepora complanata* forms flat, upright sheets with undulating or porous margins that are arranged more or less close to each other depending on the hydrodynamic conditions and the space available for growth. Colonies are usually oriented parallel to the current direction. *M. complantata* prefers less turbulent water than *M. squarrosa* does and is, therefore, of much finer and more delicate construction. Recent ecological variation of *M. complanata* investigations (DE WEERDT 1981; WEDLER 1984) show that *M. squarrosa* is a colonial variation of *M. complanata. Millepora alcicornis* differs from the other two species by more intensive branching. The main stem and main branches of the colony have a round diameter. More marginal branches may anastomose and form porous sheets. Of the milleporans of the region, *M. alcicornis* lives in the most protected environment.

Fig. 5 demonstrates that colonies of *Millepora* not only differ from one species to the next but are highly variable within a single species. Colony shape depends on differences in water currents and light/depth. Due to the great variability present in the morphology of a single species, different species cannot yet be clearly kept apart. The taxonomy of *Millepora* is still problematical. The study of the nematocysts of all the numerous growth types of *Millepora* reveals the necessity of a review of the taxonomy of the fire corals of the Caribbean. Whereas *M. squarrosa* is an ecological form of *M. complanata*, *M. alcicornis* probably consists of up to 9 species (WEDLER 1984). The taxonomic problem is caused by overlapping ecological and genotypic growth types.

Halocordyle disticha GOLDFUSS 1820 is a cosmopolite species of tropical and temperate marine environments. It is characteristic of strongly illumitated areas and can tolerate large differences from shaded to sunny mostly shallow water, where only few other hydroids can compete as well against the Chlorophyceae. In weakly turbulent surface water of the reef or the artificial constructions of the harbour the maximal colony size is found, whereas in areas with strong surf and in deeper more shaded zones colonies remain small. *H. disticha* avoids being overgrown and covered by algae by escaping movements of marginal portions of the colony as shown in Fig. 2.

The clavidid hydroid *Rhizogeton fusiformis* AGASSIZ 1862 settles only in a very special niche, the calcareous algae *Amphiroa fragilissima* and other related species that grow in small enclaves of *Millepora squarrosa*. All such algal growths on isles on the calcareous skeleton of *Millepora* may show this hydroid. *Corydendrium parasiticum* LINNAEUS 1767 is found in extremely dark spots in the rocky littoral. Its hard parts are a preferred substrate for some other hydroids like *Cuspidella humilis* and *Filelum serratum*. *Turritopsis nutricula* MCCRADY 1856 is a cosmopolitan species of the tropics and occurs in illuminated and also in shaded areas from the sublittoral zone to areas of greater depth. The size of the colony increases with depth. *Garveia cerula* CLARKE 1882 lives in tropical and temperate brackish water in the littoral zone of all the world oceans. It is dominant in the hydroid fauna of the Ciénaga Grande lagoon growing in the eulittoral zone just below low water line. Given favourable conditions, colonies may reach a hight of 15 cm.

The tubulariid hydroid *Zyzzysus solitarius* WARREN 1906 is found in the shaded surf area living only on sponges (*Tedania* sp.). The eudendridid (tree-like) hydroid *Eudendrium carneum* CLARKE 1882 lives in shaded and half-shaded areas of the sublittoral. Here it prefers exposed spots in which currents are continuous and strong. In the deeper sublittoral below 15 m depth the only surfaces that have been settled on are those that have been exposed to the current. In the upper sublittoral zone colonies are often suffocated by chloropyceen algae (Fig. 2). Ideal shapes of *E. carneum* colonies form in great depths, under special conditions i. e. a cave or the lower side of the harbour jetty perfect shapes may also develop. *Eudendrium ramosum* LINNAEUS 1758 colonies are more delicately constructed than those of *E. carneum*. *E. ramosum* lives in shaded areas of the rocky shore and reflects hydrodynamic conditions well in shape and size of colonies. *Myrionema hargitti* CONGDON 1907 contains symbiontic algae and is, therefore, restricted in its occurrence to the illuminated zone in shallow water below 1 m depth. The turtle grass (*Thalassia*) and roots of mangrove just above the sandy substrate are favoured environments. *Myrionema* tolerates much transport of sand and detritus in its place of attachment.


cm/sec
30-50
20-30
10-20
5-10
<5
current velocity
M. squarrosa
M. complanata
M. alcicornis

The haleciid, tree-like hydroid *Halecium bermudense* CONGDON 1907 directs its branches vertically to the current. It prefers illuminated water with constant and calm currents. Colonies of *Halecium halecium* LINNAEUS 1758 can commonly be found attached to sponges and are in this case of small size. Large forms are found in sheltered rocky regions. *Halecium muricatum* HINCKS 1868 settles secundary hardgrounds and other hard substrates on muddy sand with weak or medium strong currents.

The campanulinidid *Lovenella gracilis* CLARKE 1882 attaches itself exclusively to the shells of the toxoglossan gastropods *Terebra taurinus* and *Crassispira* sp. living on sand. During the day the hydroids disappear with their host into the substrate, closing thecae with acute opercula. At nighttime the hydroid becomes active when the gastropod has left its hiding place in the sand and crawls on the substrate in search of food.

The campanulariidid grass-like *Campanularia columbiana* WEDLER 1976 lives exclusively on the eel grass *Syringodium filiforme* that grows on sand in the bays at 3-4 m depth. *Campanularia lennoxensis* JÄDERHOLM 1904 attaches itself to the inner section of the thalli of *Sargassum* that is attached to rocky substrates within the area of surf. The small and branched colonies of *Obelia dichotoma* LINNAEUS 1758 live on hydroids and other sedentarians in the shaded and current swept littoral zone. This rapidly growing and reproducing species during dry seasons enters the estuarine zone. *Obelia geniculata* LINNAEUS 1758 represents a typical species that populates algae (*Sargassum vulgare*) and rocks within the surf zone. Individuals of this species are adapted to rapid growth and maturity and thus remain small. They settle on all new algal substrates within a short time.

The sertulariidid *Cnidoscyphus marginatus* ALLMAN 1877 is very variable in shape and size and represents a dominant form among the hydroids of the littoral zone of Santa Marta. It reflects faithfully the different ecological conditions involved (Fig. 3) (WEDLER 1975). It settles the base of the surf area to the lower zone of the sublittoral. Perfect colony shapes depend on environmental pressures. A nearly ideal morphology is found at greater depth as well as in very shallow water below the jetty construction. *Thyroscyphus ramosus* ALLMAN 1877 prefers rock overgrown with phaeophyceans that are scattered on the sand within turtle grass. Although its average size ranges between 8 and 12 cm, *T. ramosus* may reach a length of 60 cm in protected sea grass.

Idiellana pristis LAMOUROUX 1816 lives in shaded regions of the rocky littoral with constant current conditions and is found on cliffs as well as in the reef and on the jetty. *Diphasia digitalis* BUSK 1852 prefers strongly shaded rocky environments, especially caves. *Diphasia tropica* NUTTING 1904 lives on phaeophyceans in the area of surf. *Idiella* and *Diphasia* are usually damaged and ragged in their normal niches

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◀ Fig. 5. Colonies of *Millepora* do not only differ between the species, but also react to light and current differences within each species with morphological changes.

Abb. 5. *Millepora*-Kolonien unterscheiden sich nicht nur von Art zu Art, sondern sind auch innerhalb einer Art sehr unterschiedlich, wenn Licht- und Strömungsbedingungen verschieden sind.

on the rocky shore. On the inside of caves or below the jetty they develop large monospecific growth of more than 1000 cormi in contrast to the 3 or 4 on the rocky shore. This demonstrates that the actual place of this species within the community and their ecological optimum differ considerably.

Dynamena crisoides Lamouroux 1824 is one of the few hydroids living in the intertidal zone and is found below overhanging rocks within the surf and swing zones. Non branching colonies of *Dynamena cornicina* McCrady 1857 live on algae and the hard basal portions of other hydroids, or within the rocky surf area and just below it. In sandy environments it settles on *Thalassia testudinum* as well as on *Syringodium filiforme*. *Dynamena quadridentata* Ellis & Solander 1786 is only present on the basal portions of *Sargassum* and on rock near its attachment in the infralittoral fringe of the rocky shore exposed to surf. *Sertularella speciosa* Congdon 1907 is characteristic for the shaded regions of the rocky shore, reef and harbour constructions. The colony is of a two-dimensional construction and has branches directed in a right angle to the current. From the area below surf zone to deeper, quieter regions colonies become larger. *Sertularia inflata* Versluys 1899 settles on shady and strongly current swept rocks as well as on sea grass. If illumination increases to over 20% of the light that penetrates the water surface, *S. inflata* can no longer compete against algae (Wedler 1975). The size of colonies is quite variable and depends on the strength and direction of the currents.

Plumulariidae, like *Antennella gracilis* Allman 1877, are feather-like hydroids living in a quiet habitat on hard substrates like rocks, the shell-spines of bivalves such as *Spondylus*, the hard basal parts of hydroids. The very delicate colonies can tolerate only week currents but can dispose of detritus that may settle on them from the suspension with the aid of mobile stalks (cauli). In the upper region of the rocky shore well illuminated and strongly current swept portions are usually settled on by *Halopteris diaphana* Heller 1868 (carries zooxanthellae), but extreme locations are avoided. Colonies are mainly attached to algae, less commonly also to the basal parts of other hydroids. *Halopteris carinata* Allman 1877 lives on sponges and dead gorgonians in depths below 5 m in a rocky habitat that is exposed to strong currents.

Monotheca (Plumularia) margaretta Nutting 1900 is only attached to the eel grass *Syringodium filiiforme* in 2-3 m depth. *Plumularia habereri* Stechow 1909 forms up to 30 cm large colonies and lives in the current swept zone of the rocky shore. The colonies themselves are often populated by *Parazoanthus tunicans*. *Plumularia halecoides* Alder 1859 commonly occurs on secundary hardgrounds and on roots of mangrove bushes in moderate swell. Individuals of *Plumularia setacea* Linnaeus 1758 live in small niches and narrow channels within the extremely exposed rocky shore. Here they form small patches which are never exposed to direct surf. *Plumularia strictocarpa* Pictet 1893 lives on phaeophyceans and *Thalassia* in the surf and current swept regions of the shore. Of all the hydroids, *Aglaophenia latecarinata* Allman 1877 tolerates most surf and lives mainly on algae like *Sargassum*, but also in small niches, cavities and channels within the turbulent zone. Like *Plumularia setacea*, *A. latecarinata* is a small feather-like hydroid of the surf zone that needs to move backwards and forwards a little and is not found in areas with unidirectional currents. *Lytocarpus philippinus* Kirchenpauer 1872 is common in all tropical seas on rocks from the wave zone into deeper current regimes on cliffs, reefs and harbour jetties.

Habitats and Zonations.

Strongly Exposed Rocky Limestone Cliff.

The well terraced cliff of Playa Brava (Fig. 1, loc. 5) is formed on cemented calcareous dune sand (beachrock) resting on metamorphic rock. Two terraces are present connected to a slope that is studded with sharp peaks on a roughly eroded surface. Up to 80 cm wide and 1.5 m deep pits have been eroded into this slope each with inward rising sides and a shallow rock pool at their base (Fig. 6). The swell of the open sea pounds against the cliff continuously. The cliff is subject to rather severe exposure during Brisa time when the easterly trade winds push waves of 2 to 4 m hight against the shore. During rainy periods only the lower part of the cliff is moistened by splash and spray and the upper terrace is totally dry. Its surface is covered with crystallized salt and only *Cenchritis muricatus* (32) is present on its proper. On the more seaward side, in calm seasons, dried out spray pools contain *Nodilittorina tuberculata* (27) encrusted by salt covering the bottom.

The bare rock of the upper terrace graduates into yellow and black rock on the slope. Here the walls of the shallow rock pools are smooth and populated by *Nodilittorina tuberculata* even when the salinity of the water increases and the temperature is high. When salinity and temperature rise too much, the individuals of the species leave the pool but remain in the wet zone near the water surface. On the pitted walls above the pools *Nerita peloronta* (19) is found. Near lower pools *N. versicolor* (17) joins *N. peloronta*. A narrow overlap is also present between *Nodilittorina interrupta* (31) populations mainly in the yellow zone and *N. ziczac* (26) populations in the black zone.

The later populations end in the upper green zone, closely correlated with the uppermost presence of *Purpura patula* (80). The green zone is periodically splashed or kept moist by spray. It ends on the intertidal platform that is raised at its seaward edge by a crust of porous limestone continuously reconstructed and built up by *Lithothamnium*. This lower platform, is therefore flooded by water in shallow pools refilled by splashes at low tides and waves at high tide or wind. Here *Petaloconchus varians* (38) forms microreefs. *Littorina meleagris* (28) moves through pools and across algal tufts and mosses. *Acmaea pustulata* and *Collisella antillarum* (7) are attached to rocky substrates as well as to the operculum of *Cittarium pica* (8). The later comes onto the platform when it has been dampened by splashes and retreats further down at periods of calm low water. Its occurrence coincides more or less with that of *Chiton marmoratus* (1). *Acanthopleura granulata* (2), in contrast, does not leave the intertidal terrace in seaward direction, but enters the steep green splash zone. The *Lithothamnium* crusts of the platform, especially those on the edge, are grazed by *Fissurella nodosa* (5). *Leucozonia ocellata* (102) hunts on the platform while *Leucozonia nassa* (101) follows below, continuing down into the zone of *Echinometra* rock hiding holes that occurs in the deepest wave troughs.

Exposed Cliff of Metamorphic Rock.

The small island Isla Morrito (Fig. 1, loc. 9) lies opposite to the marine Station of Santa Marta. Its cliffs are exposed to the swell of the sea, which is stronger on the seaward side and less severe on the landward side. Zonation is very similar to that

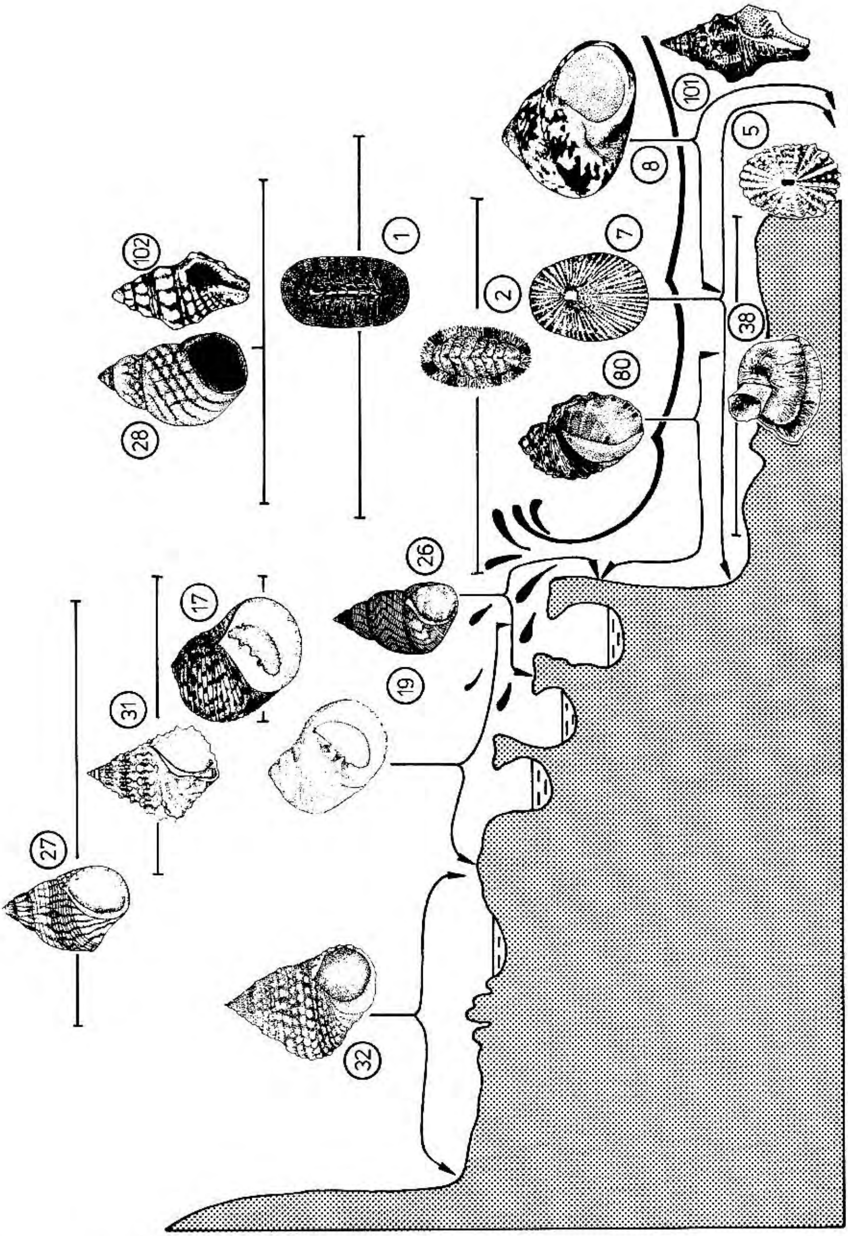


Fig. 6. The strongly exposed rocky limestone cliff of Playa Brava is moistened by splash, and its supratidal zone is pitted by pools. The intertidal area shows a platform with a steep drop-off into the subtidal zone. Mollusc zonation is well developed.

Abb. 6. Am stark der Brandung ausgesetzten Kliff von Playa Brava wird der Fels bis weit hinauf von Spritzwasser genäßt; Spritzwassertümpel fangen das Wasser auf. Der Gezeitenbereich besteht aus einer Plattform, die zur See hin steil abstürzt. Mollusken sind deutlich in Zonen angeordnet.

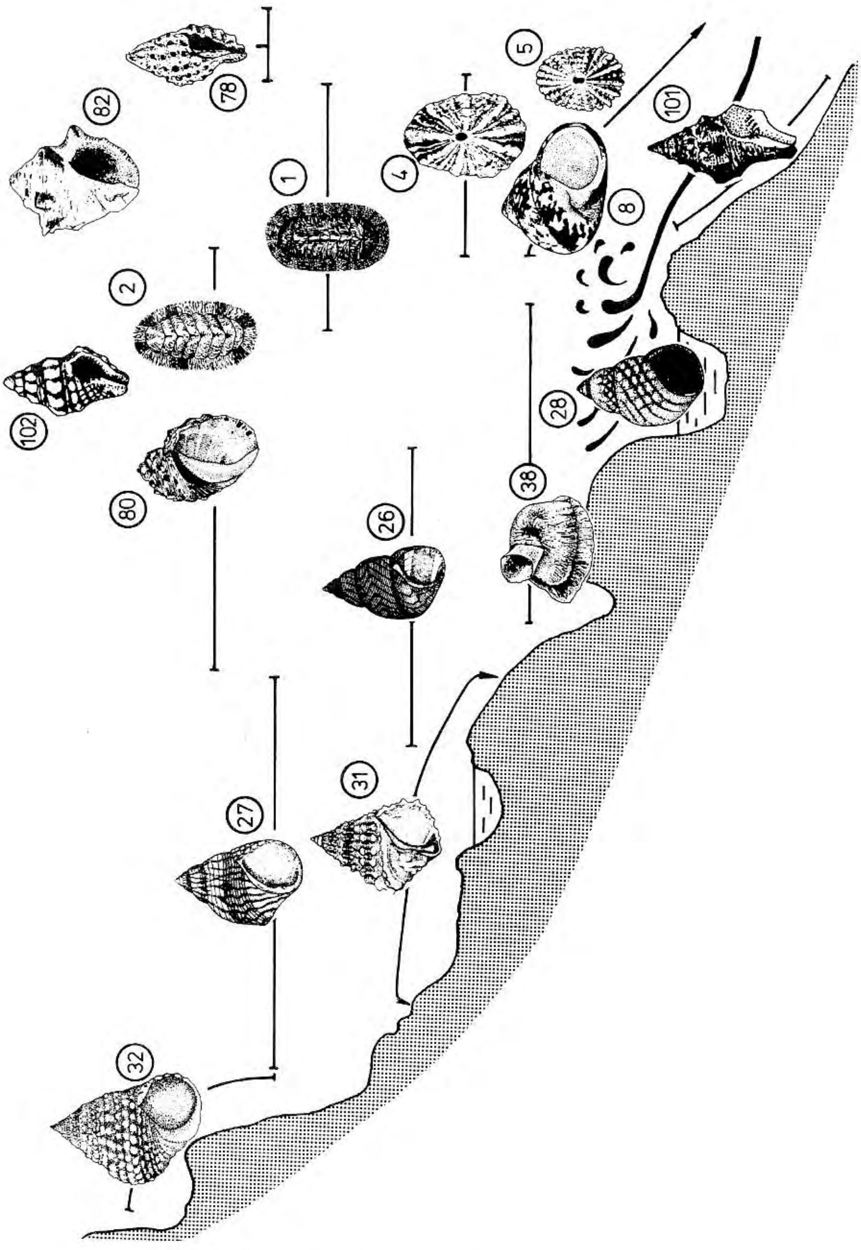


Fig. 7. The exposed cliff of the Isla Morrito consists of metamorphic rock that results in a less conspicuous morphological zonation, but the biological zonation is as clear-cut as on the limestone cliff (Fig. 6).

Abb. 7. Die der Brandung ausgesetzte Felsküste der Insel Morrito besteht aus metamorphem Gestein und zeigt daher keine deutliche morphologische Untergliederung. Die biologische Zonierung ist dagegen genauso scharf ausgeprägt wie an Kalkfelsen (Abb. 6).

found on the cliffs of the Playa Brava, but a terraced profile is not well developed in this mainly silicious rock (Fig. 7).

The uppermost platform was mainly formed by salt erosion and is populated by *Cenchritis muricatus* (32). On the upper slope to the next platform *Nodilittorina interrupta* (27) is present, replaced by *N. ziczac* (26) on the lower slope. Both are well hidden in the pitted rocky surface, dyed black by blue green algae. Spray water pools are filled with water that often deviates considerably from the normal sea water in temperature and salinity. They contain *Nodilittorina tuberculata* (31) and young *N. interrupta.*

Petaloconchus varians (38) is attached to the walls of surf channels. Here also *Acanthopleura granulata* (2) and *Purpura patula* (80) are present. The occurrence of *Purpura patula* overlaps considerably with that of *Nodilittorina ziczac* because of the very irregular topography of the rocky surfaces.

Pools in the wash zone contain numerous *Littorina meleagris* (28). On the wave swept intertidal edge of the cliff *Cittarium pica* (8), *Chiton marmoratus, C. tuberculatus* (1), *Fissurella nodosa* (5) and *Leucozonia nassa* (101) are found. Hidden among algal thickets *Fissurella angusta* (4) is fixed to the rock and *Leucozonia ocellata* (102) searches for prey. *Thais deltoidea* (82) and *Morula nodulosa* (78) populate the zone of the crust forming calcareous algae just below the intertidal zone down to the bore holes of the *Echinometra* zone.

Punta de Betin — Moderately Exposed Rocky Shore.

The marine station of Santa Marta is built on a peninsula that is less exposed to the waves from the southern to the western shores (Fig. 8). Arrow width indicates decreasing current action of the surf from south to west and water movement and the surf is characterized at the left from violent to weak. With decreasing exposure the average grain size decreases from boulders to sand. The most typical and most visible hydroids and gastropods for the different parts of the shore are listed. The following figures (9-14) present more detailed sections of this coast ranging from coarse to fine sediment and from exposed to sheltered conditions.

Boulder Zone with Moderate Exposure.

The rocky cliff to the south of Punta de Betin (Fig. 9) is less exposed to waves than the cliffs of the island Morrito. Supra- and intertidal gastropod-zones are narrower here and *Nodilittorina interrupta* (31) and *N. ziczac* (26) form mixed populations. *Nerita versicolor* (17) intermediates to the intertidal zone with *Fissurella nodosa* (5), the three large chitons *Acanthopleura granulata* (2), *Chiton tuberculatus* and *C. marmoratus* (1), *Nerita tessellata* (20), *Purpura patula* (80) and young individuals of *Cittarium pica* (8). The area of continuous action of surf of the lower eulittoral and the infralittoral fringe is populated by a number of hydroid species listed in an order that reflects decreasing resistance to exposure *Aglaophenia latecarinata, Plumularia setacea, Zanclea costata, Sertularia inflata, Dynamena cornicina* and *Cnidoscyphus marginatus.*

The zone of oscillating wave turbulance is characterized by *Fissurella angusta* (4) and *Ceratozona rugosa* hidden among algal tufts, *Hemitoma octoradiata* (6), *Thais deltoidea* (82), *Morula nodulosa* (78), *Leucozonia nassa* (101) with shells covered by

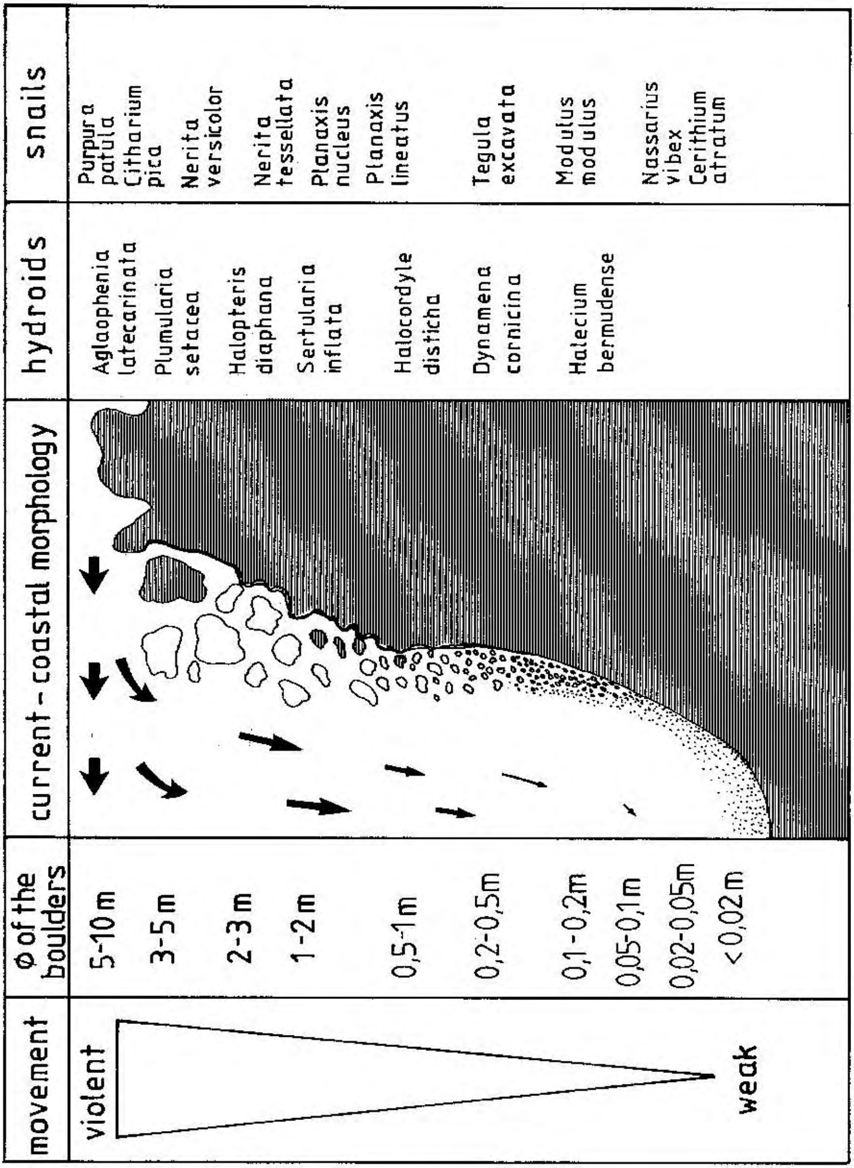
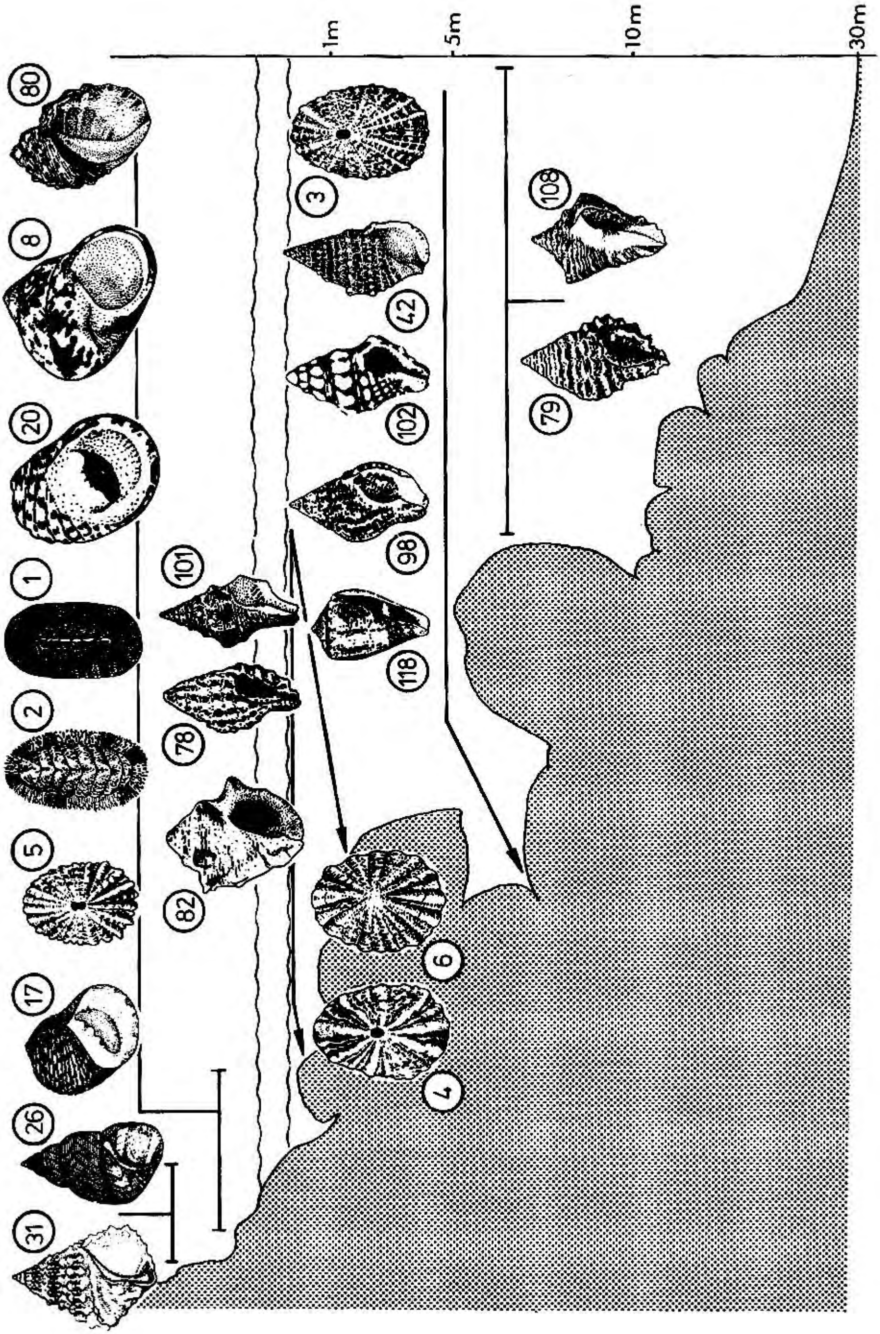


Fig. 8. Rocky shore of Punta de Betin. — Details in Figs. 9-14.

Abb. 8. Felsküste von Punta de Betin. — Detailbilder in Abb. 9-14.

crusts of calcareous algae; with *Conus mus* (118), *Pisania auritula* (98), *Leucozonia ocellata* (102), *Cerithium litteratum* (42) and *Diodora listeri* (3) in the crevices, cracks and the pits dug by *Echinometra*. Here, in the uppermost sublittoral zone,


-1m
-5m
-10m
-30m
80
8
20
1
2
5
17
26
31
101
78
82
3
42
102
98
118
6
4
108
79

zoanthids, hydroids, madreporids and octocorals are common. The zone of oscillating currents has also been settled on by numerous hydroids, listed from exposed to protected: *Halopteris diaphana, Turritopsis nutricula, Halocordyle disticha, Sertularella speciosa* (small forms) and *Cnidoscyphus marginatus.*

Below this zone *Ocenebra rosea* (79) is common and an occasional *Vasum muricatum* (108). Unidirectional currents now prevail and hydroids such as *Halopteris carinata, Cnidoscyphus marginatus, Lytocarpus phillippinus, Eudendrium carneum, Gymnangium speciosum, Sertularella speciosa* (large forms), *Aglaophenia allmani* and *Plumularia habereri* are present, listed in the order of their decreasing resistance to currents.

Sublittoral Cliff and Cliff Bottom.

Between Punta de Betin and Isla Morrito, in 2-5 m depth (Fig. 10), the dominant faunal element is *Gorgonia ventalina.* On these sea fans *Cyphoma gibbosum* (62) and *Simnia acicularis* (61) are regularly present. *Coralliophila caribbaea* (85) parasitizes the tissue of the roots of the gorgonian. The hydroids *Halocordyle disticha, Turritopsis nutricula, Halecium halecinum, Cnidoscyphus marginatus, Halopteris carinata, Lytocarpus philippinus* are also present.

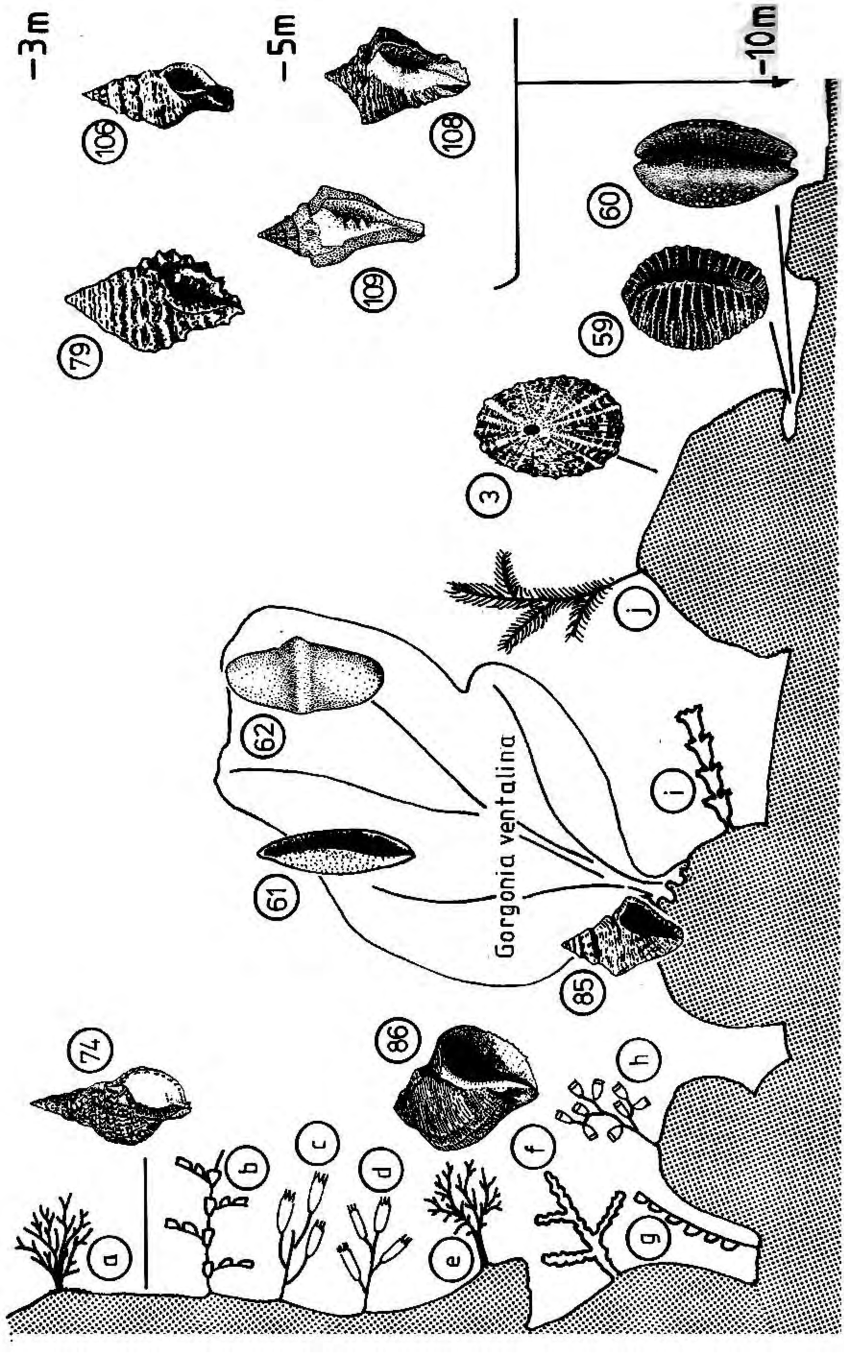
Boulders in the upper part of the zone may be partly or totally covered by the colonial, crust forming zoanthid sea anemone *Palythoa caribbaea* with the tubes of *Petaloconchus erectus* projecting from them. The hydroids *Halocordyle disticha, Turritopsis nutricula* and *Halecium halecinum* are common here. A very small hydroid (*Halecium* n. sp.) lives attached to the most exposed part of the surf zone. On small algae it is omnipresent in all rocks of the region that are exposed to extreme movements of waves.

Between boulders and rocks within the zone of *Palythoa* and *Gorgonia* there are numerous caves with walls covered by sessile organisms, among them the hydroids *Dynamena crisoides, D. cornicina* and *Sertularia inflata* (= *S. marginata*). The gastropods *Cypraea cinerea, C. spurca acicularis, Trivia pediculus* (59), *Diodora cayenensis, D. listeri* (3), *Lucapina suffusa, Ocenebra rosea* (79) and the chitons *Ischnochiton pectinatus* and *Acanthochitona spiculosa* feed on the organisms of the cave walls.

Corals may grow on boulders and rocks and continue below the *Gorgonia* zone down to 20 m depth. On them *Coralliophila abbreviata* (86) and between and below them *Cypraea cinerea, C. cebra* (60), *Ocenebra rosea* and *Latirus angulatus* (106) are present. Large gastropods *Tubinella angulata* (109) and *Vasum muricatum* (108) regularely come into this environment from the sand flats below, *Charonia variegata* (74) also appear, but less frequently. Here the hydroids *Turritopsis nutricula, Eudendrium carneum, Ectopleura grandis, Cnidoscyphus marginatus, Plumularia habereri* and *Lytocarpus philippinus* are common.

◀ Fig. 9. Boulders in a moderately exposed rocky cliff to the south of Punta de Betin show narrow supra- and intertidal zones, and a wider zone of oscillating turbulence.

Abb. 9. Der Geröllstrand der Steilküste südlich von Punta de Betin ist der Brandung nur bedingt ausgesetzt und zeigt somit einen schmalen Spritzwasser- und Gezeitenbereich, der von einer etwas breiteren Schwingungszone begleitet wird.


-3m
-5m
-10m
74
79
106
109
108
86
85
61
62
3
59
60
Gorgonia ventalina
a
b
c
d
e
f
g
h
i
j

Sargassum Attached to the Infralittoral Rocky Fringe.

Sargassum vulgare is attached to rocks in the surf zone within the lowermost eulittoral and the uppermost sublittoral on the western side and the southern front of the cliffs of Punta de Betin (Fig. 11). Even though algae are destroyed by extreme surf each year, they are the habitat for a varied gastropod and hydroid fauna.

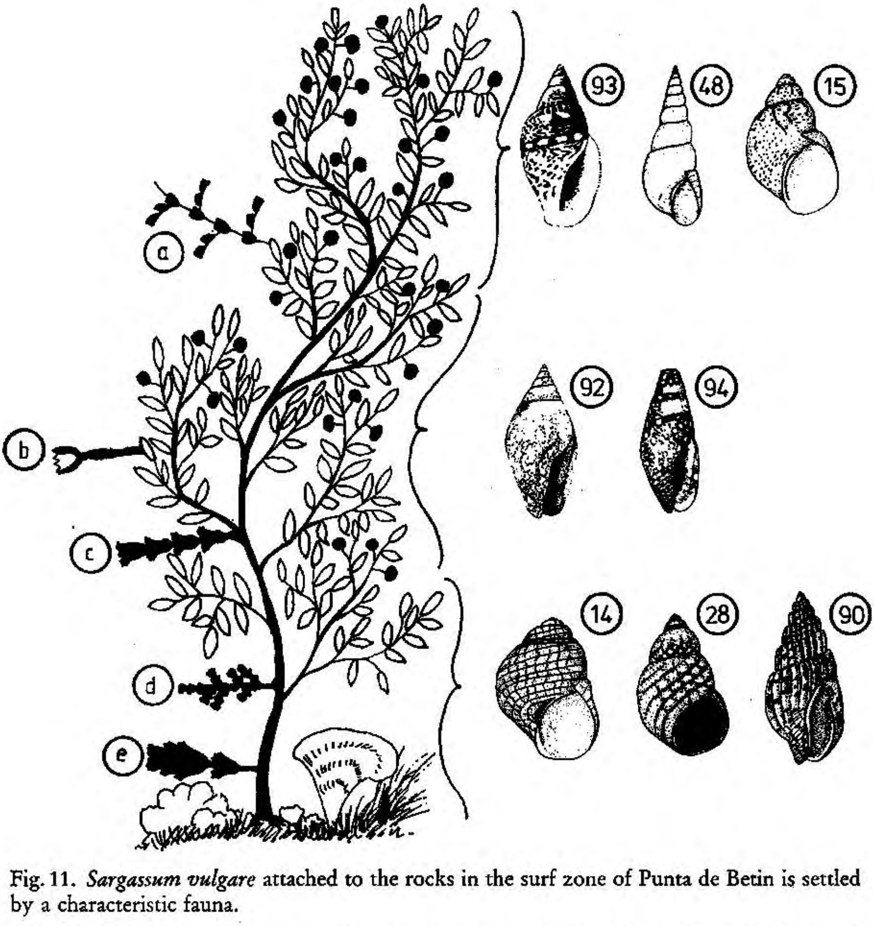


Fig. 11. *Sargassum vulgare* attached to the rocks in the surf zone of Punta de Betin is settled by a characteristic fauna.

Abb. 11. Der Seetang *Sargassum vulgare* wächst im Gezeitenbereich von Punta de Betin und ist von einer typischen Fauna besiedelt.

◀ Fig. 10. Sublittoral cliff and cliff bottom between Punta de Betin and Isla Morrito provide holdfast and hideout for numerous sessile animals and their predators.

Abb. 10. Sublitoral Felshänge und Steinböden zwischen Punta de Betin und Isla Morrito sind dicht besiedelt von sessilen Tieren und anderen, die sich von diesen ernähren.

The most common snails are *Nitidella laevigata* (93), *Alaba incerta* (48) and *Tricolia affinis* (15). In addition *Nitidella nitida* (92) and *Mitrella ocellata* (94) are usually present, although their main occurence lies on the rocks to which *Sargassum* is attached. Individuals of *Phyllaplysia engeli, Stylocheilus longicauda, Elysia ornata* and *Scyllae pelagica* are regularly present in smaller numbers. Other species such as *Mitrella argus* (95), *Mitrella lunata* (96), *Tricolia tessellata* (14), *Anachis sparsa* (90), *Littorina meleagris* (28) and *Aglaja evelinae* may be found in small numbers. Juveniles of *Hemitoma* and several neogastropods may also be present.

The hydroid *Clytia simplex* (b) settles *Sargassum* weed directly by way of larvae (planulae), *Halopteris diaphana* (a) enters the weed by way of hook-like stolones from the rocky substrate. *Dynamena cornicina* (c), *Sertularia inflata* (d), *S. marginata*, and *Dynamena quadridentata* (e) settle on *Sargassum* by stolones encroaching from the rock onto the base of stem of the algae, or directly via larvae.

Pure Pebble and Boulder Beach.

In the transition from the boulders of the western side of Punta de Betin to the southern shore (Fig. 12) a well developed gastropod zonation is found. It differs from that of boulders and cliffs but also from that of pebbles associated with sand.

Tegula excavata (10) is found above and *Mitrella ocellata* (94) and *Tegula viridula* (9) just below wave line. Below 0.5 m depth the place of *M. ocellata* is taken by *Nitidella nitida* (92). From here onward *Modulus modulus* (41) is seen grazing on the upper side of rocks and pebbles while their lower sides provide shelter and food for *Anachis obesa* (87), *Anachis brasiliana* (88) and *Anachis sparsa* (90). These lower rock surfaces also are the attachment place for the short and solid colonies of the hydroids *Dynamena cornicina* and *Sertularella robusta*, as well as for the limped *Hipponix antiquatus* (50).

Rocky Beach with Sand.

Where boulders and pebbles lie on gravel and sand, as is the case on the shore below the stairs of the marine station (Fig. 13), the gastropod fauna again changes in its composition. In the intertidal zone *Planaxis nucleus* (40) and *Tegula excavata* (10) are present. In the lower eulittoral and the upper sublittoral fringe rocks show a dense population of *Mitrella ocellata* (94) and *Planaxis lineatus* (39). The accompanying fauna consists of *Tegula viridula* (9), different species of *Caecum* (34), *Nerita tessellata* (20), *Modulus modulus* (41), *Cerithium atratum* (43), *Anachis brasiliana* (88), *Pisania auritula* (98), *Persicula lavalleana, Hyalina avena* (116), *Persicula pulcherrima* and *Chiton tubercularis* (1).

The lower sides of rocks in the upper sublittoral contain a large population of *Nitidella nitida* (92). Besides individuals of this species a fauna of many other species is present, including the chitons *Chiton tubercularis, Ischnochiton striolatus,* the limpets *Collisella antillarum* (7), *Fissurella angusta* (4), *Diodora listeri* (3), *Hipponix antiquatus* (50), the trochid *Calliostoma sarcodum,* the tonnaceans *Cymatium nicobaricum* (71), *C. pileare, Bursa granularis cubaniana* (73), the neogastropods *Morula nodulosa* (78), *Aspella anceps, Engina turbinella, Pisania tincta, Dolicholatirus cayohuesonicus, Colubraria swifti, Anachis brasiliana, A.*

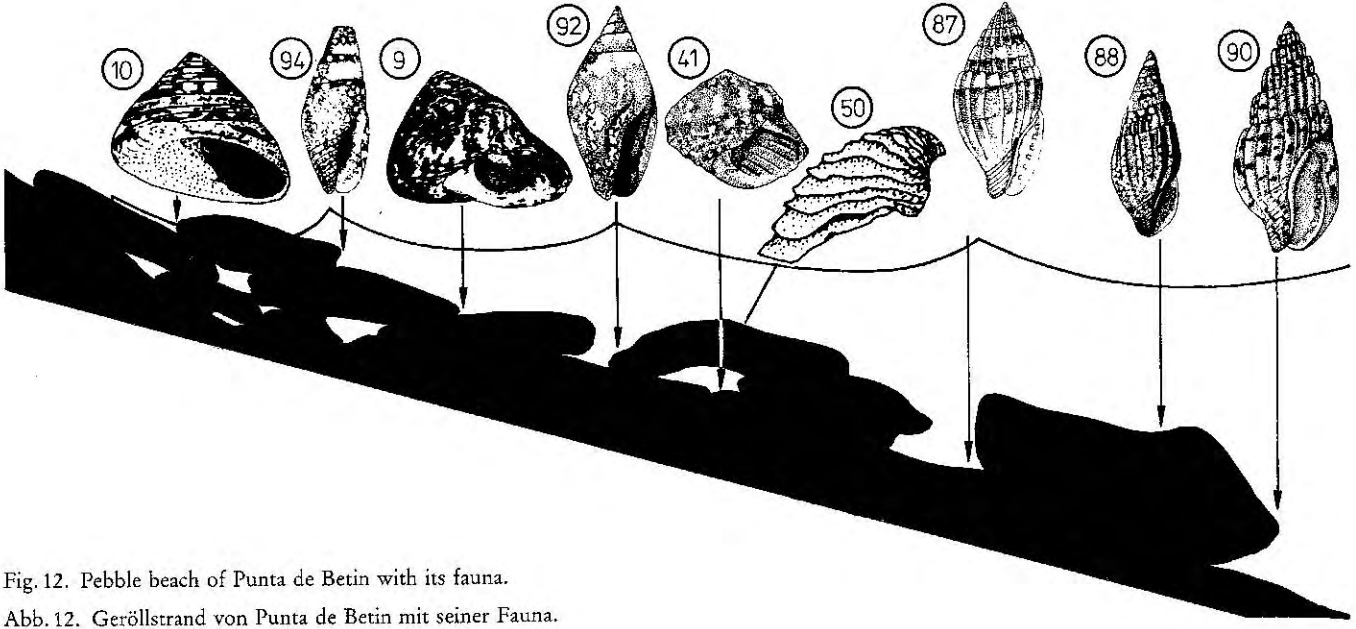


Fig. 12. Pebble beach of Punta de Betin with its fauna.

Abb. 12. Geröllstrand von Punta de Betin mit seiner Fauna.

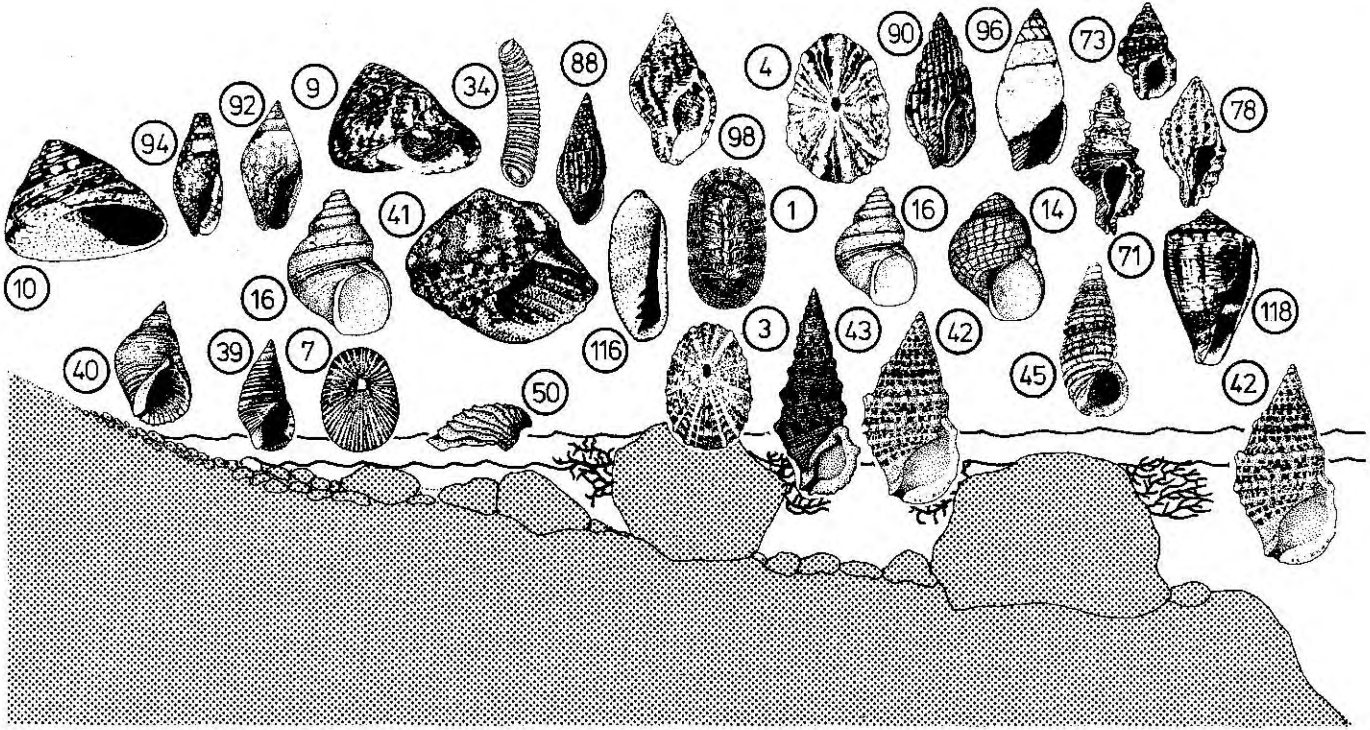


Fig. 13. The boulders and pebbles of the beach below the biological station at Punta de Betin rest on sandy bottom. The tidal area is here well zoned and a very wide spectrum of species is present.

Abb. 13. Der Strand direkt unter der biologischen Station auf Punta de Betin zeigt große und kleine Gerölle mit Sand dazwischen. Hier ist eine klare Zonierung im Gezeitenbereich anzutreffen und eine besonders reiche Artenvielfalt entwickelt.

sparsa (90), *Mitrella lunata* (96), *Drillia solida, Crassispira albumaculata* and *Conus mus* (118), and the opisthobranchs *Aglaja evelinae, Berthella agassizii, Taringa telopia, Pleurobranchus testudinarius, Dendrodoris krebsii, Chromodoris neona, C. perola, Peltodoris hummelincki igla, Phidiana lynceus* and *Spurilla neapolitana.*

Here, algal growths covering rocks and sand provide living space for *Tricolia bella* (16), *T. tessellata* (14), *Diastoma varium* (45), *Cerithium atratum* (43), *C. litteratum* (42) and juveniles of *Strombus.* Algal mosses on deeper boulders contain species of *Cylichnella, Atys, Tornatina, Caecum* and rissoids.

Gravel-Boulder Beach of Normally Quiet and Periodically Strong Exposure.

Just below the guest house of the marine station single boulders are surrounded by gravel in 0.5 to 1 m depth (Fig. 14). These boulders provide a holdfast for *Sargassum* with the typical fauna (see Fig. 11). The hydroids *Sertularia inflata* and *Dynamena quadridentata* are the most common species on *Sargassum.* The number of colonies changes from the shore seaward and the composition of populations also differs from more protected to more exposed weeds.

The gravel beach and infralittoral fringe is bordered by a rocky shore with *Pisania auritula* (98). During quiet periods dense algal thickets grow on all substrates and contain immense numbers of *Diastoma varium* (45). *Polinices lacteus* (63), *Natica livida* (66) and *Oliva reticularis* (111) are always hidden in the sediment, the first also enters gravel, while the later remain in fine grained substrates (sand, mud). *Cerithium litteratum* (42) is present on algal tufts and tickets on boulders and rocks whereas *C. atratum* (43) is found on sand and mud.

Current Washed Boulders and Piles in Quiet Water.

The sea in front of the marine station was connected to the bay of Taganguilla by a small canal situated between the rock-cliff and harbour pillars. This area is protected from waves, but always washed by currents coming from below the jetty and the bay of Taganguilla (Fig. 15).

A small platform present just above the normal intertidal range is settled on by *Nerita versicolor* (17). Within the tidal zone *Leucozonia ocellata* (102) is found. The shallow water in the shelter of rocks and concrete slabs provides hunting ground for *Pisania auritula* (98) and *Pisania pusio* (97). Numerous and extremely large individuals of *Collisella antillarum* (7) as well as *Hemitoma octoradiata* (6) settle on large concrete slabs in the intertidal zone. On harbour pilings above water line a few individuals of *Littorina angulifera* (30) can be encountered. The intertidal zone on the pillars supports small populations of *Nodilittorina interrupta* (31), *Littorina nebulosa* (29) and the limpet *Siphonaria pectinata* (126). Below the intertidal zone *Thais deltoidea* (82) and *Leucozonia nassa* (101) are present within the barnacle zone. In small depressions on the surface of the concrete, *Fissurella barbadensis* and *F. angusta* (4) are attached, just below intertidal zone and well camouflaged by algal tufts that surround and cover them. Below the harbout construction of the pier and the concrete slabs of the canal in 3-6 m depth the large gastropods *Fasciolaria tulipa* (107) and *Murex brevifrons* (77) are common.

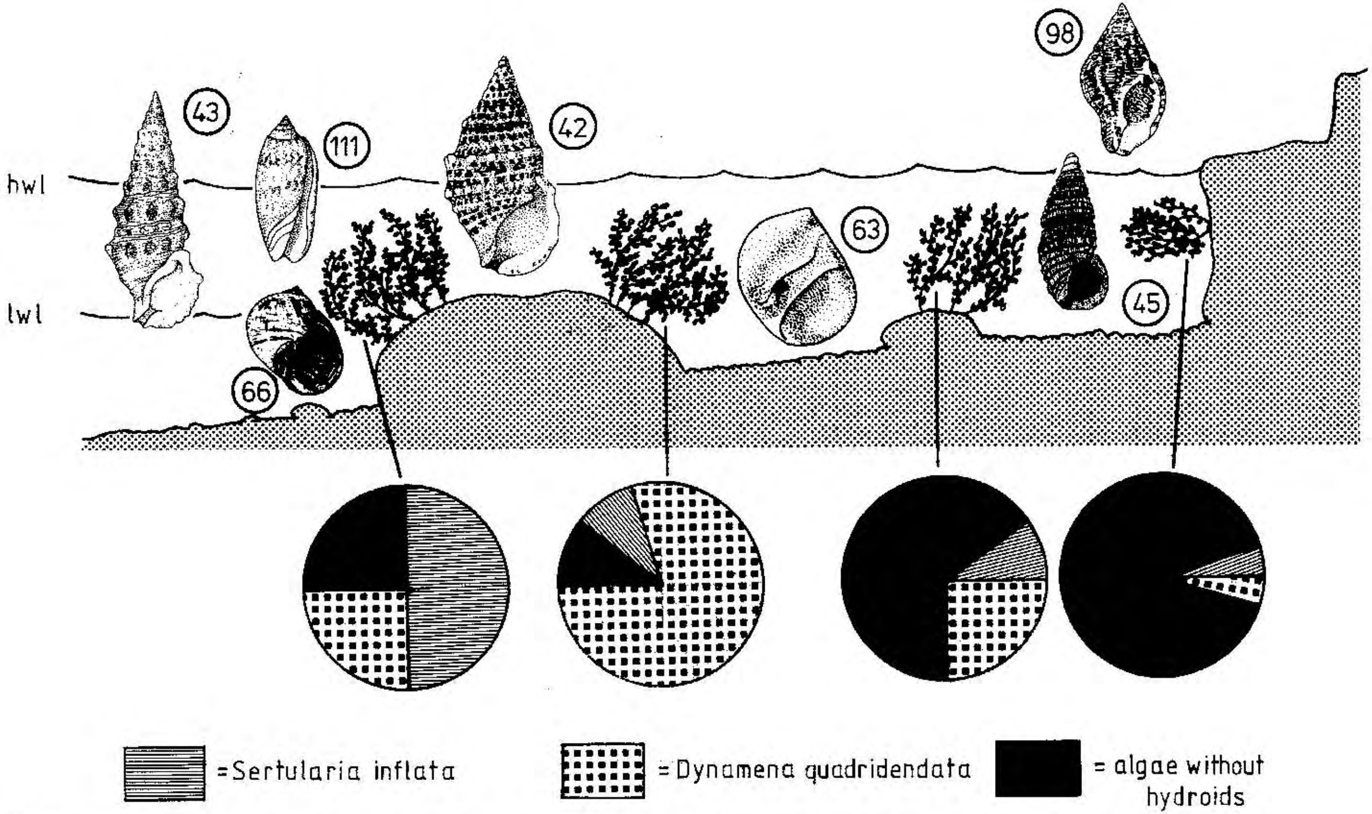


Fig. 14. Gravel-boulder beach with usually quiet water on Punta de Betin differs considerably from more exposed beaches.

Abb. 14. Block- und Geröllstrand in ruhigem Wasser unterscheidet sich hinsichtlich seiner Fauna stark vom bewegten Bereich.

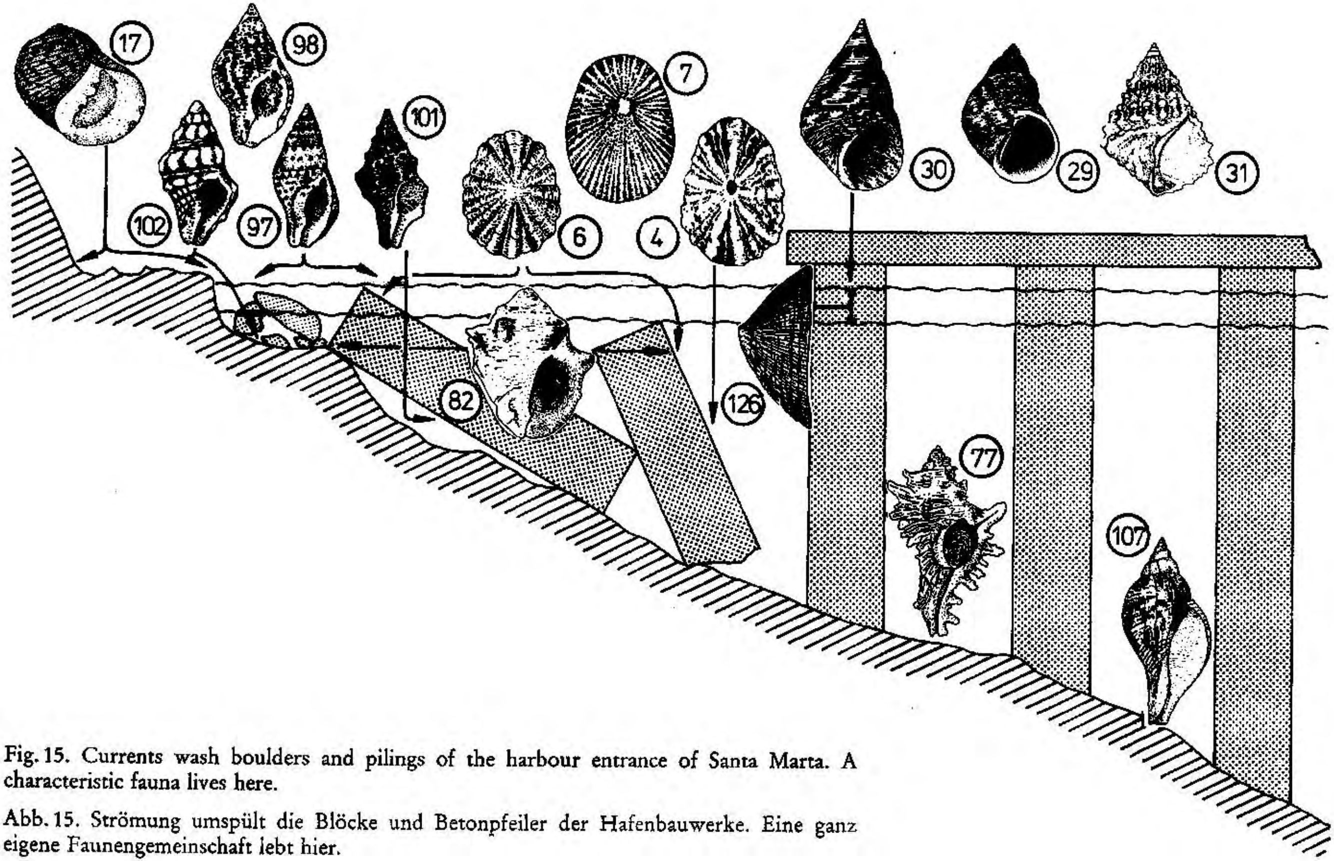


Fig. 15. Currents wash boulders and pilings of the harbour entrance of Santa Marta. A characteristic fauna lives here.

Abb. 15. Strömung umspült die Blöcke und Betonpfeiler der Hafenbauwerke. Eine ganz eigene Faunengemeinschaft lebt hier.

Artificial Cave Conditions below the Jetty.

From an ecological point of view the artificial construction of the harbour platform standing on pillars can be regarded as a variety of the rocky littoral. Conditions are comparable to a cave or a submerged overhanging cliff with optimal living conditions for sessile animals (Fig. 16). Three reasons why sessile organisms thrive well below the jetty can be given:

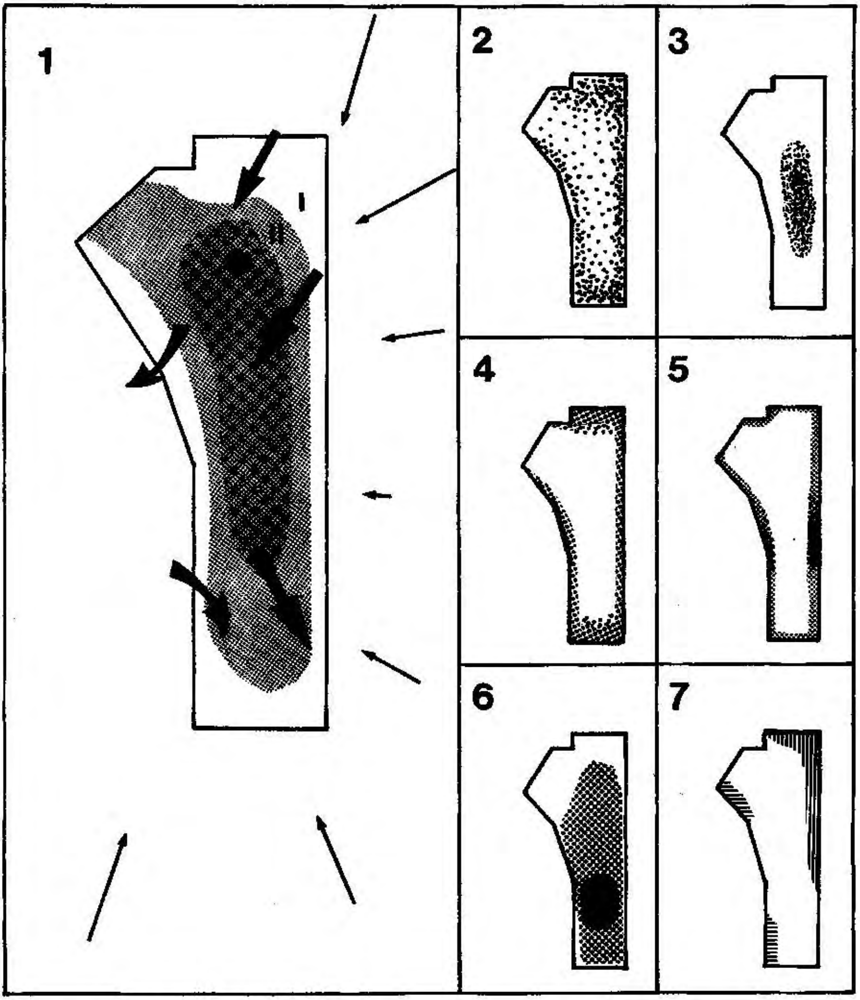
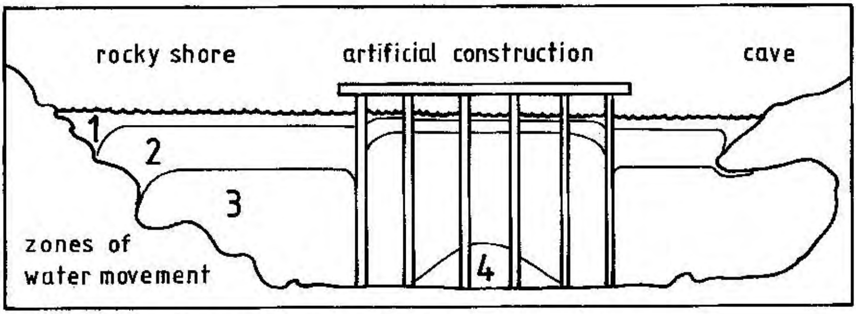


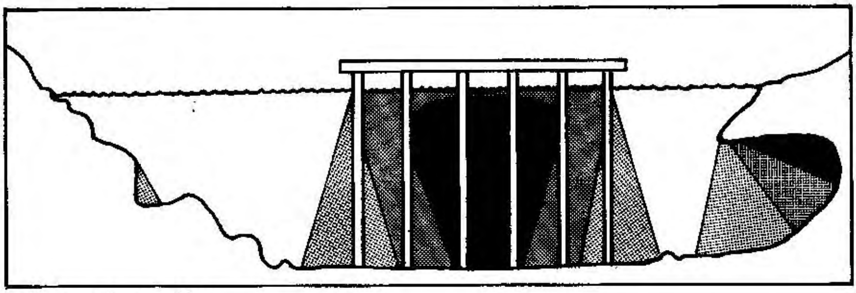
Fig. 16. Hydroid settlement of the lower submerged portion of the jetty reflects that of a large cave.

Abb. 16. Hydroiden-Besiedlung der künstlichen Höhle unter dem Hafenbetonbau.

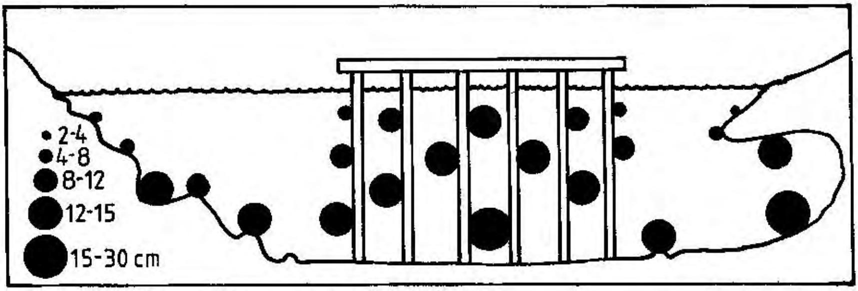
1. Surfaces are shaded and algal competition is therefore small.
2. Jetty-pillars break the waves and slow down currents. Thus hydroids can find optimal living conditions even in shallow water, which would otherwise only be given in deeper zones of the rocky shore.
3. In contrast to a cave, plankton is carried to the underside of the jetty by continuous currents. Sessile organisms are thus provided with a constant stream of abundant food.



1= turbulence; 2= oscillation; 3= current; 4= slack water



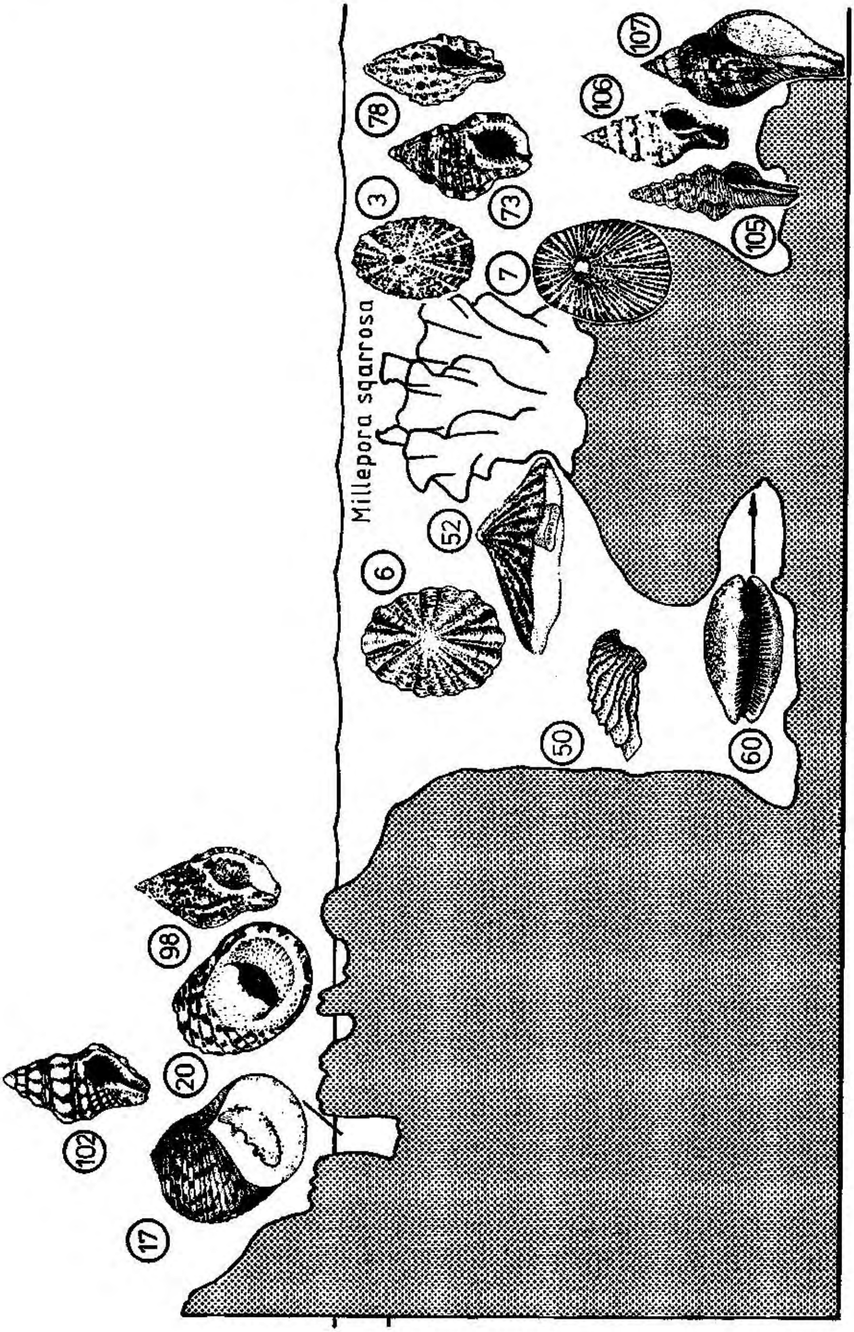
light attenuation



size of Cnidoscyphus marginatus

Fig. 17. Sessile organisms below the jetty in their zonation.

Abb. 17. Zonierung der sessilen Organismen unter dem Hafenbau.


hwl
lwl
17
102
20
98
50
60
6
52
Millepora sqarrosa
7
3
73
78
105
106
107

Water movement (Fig. 16, upper part) and light conditions (Fig. 16, central part) are directly correlated to the colony size of *Cnidoscyphus marginatus* (Fig. 16, lower part). With increasing light and increasing force of currents colonies become smaller.

Populations of Sessile Organisms below the Jetty.

Species diversity and density are higher in the artificial cave of the NW jetty of the harbour of Santa Marta than anywhere else in the area of Santa Marta due to favourable light, current and food conditions (Fig. 17).

1. Three zones of illumination can be differentiated below the concrete roof of the harbour: a) mainly stray light, but occasionally direct sunshine; b) occasional indirect rays of light; c) dark throughout. The fat arrows indicate current direction and thin arrows the direction of the daily infalling light.
2. Pattern of distribution of species of tunicates on pillars.
3. Pattern of distribution of the hydroid *Diphasia digitalis.*
4. Pattern of distribution of the hydroid *Halocordyle disticha.*
5. Pattern of distribution of the hydroid *Halecium bermudense.*
6. Pattern of distribution of the hydroid *Cnidoscyphus marginatus.*
7. Pattern of distribution of the green alga *Enteromorpha lingulata.*

Rocky Cliff in very Calm Environment.

On the cliff below the marine station toward the small bay of Taganguilla intertidal and supratidal zones almost coincide (Fig. 18), and *Nerita versicolor* (17), *N. tessellata* (14), *Leucozonia ocellata* (102) and *Pisania auritula* (98) co-occur. Close to the rocky shore in 0.5 to 1 m depth *Millepora squarrosa* covers rocks and boulders. Other hydroids such as *Dynamena cornicina* and *Sertularella robusta* are found on the lower surfaces of rocks.

When the *Millepora* colonies and rocks are turned over, a rich fauna, in which *Bursa granularis cubaniana* (73) dominates, emerges. Other gastropods found here are *Acmaea pustulata* (7), *Diodora listeri* (3), *Lucapina suffusa*, *Lucapinella limatula*, *Calliostoma sarcodum*, *Cymatium pileare*, *Favartia cellulosa*, *Aspella paupercula*, *A. anceps*, *Murex brevifrons*, *Morula nodulosa* (78). Chitons such as *Ischnochiton limaciformis* are also present. The adults of the limpet *Hemitoma octoradiata* (6) prefer the upper surface of rocks and dead milleporans, whereas *Cheilea equestris* and *Cruzibulum auricula* (52) are found on vegetated rock faces, and *Hipponix antiquatus* (50) on hard substrates in microcaves. More rarely *Cypraea cebra* (60),

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◄ Fig. 18. The rocky cliff in very calm environment, as is present between the jetty and Punta de Betin, is characterized by *Millepora* growths at very shallow depths and a very rich molluscan fauna with only little zonation apparent.

Abb. 18. In sehr ruhigem Wasser, wie es zwischen dem Betonbau des Hafens und den Felsen von Punta de Betin vorhanden ist, wachsen Milleporen in sehr flachem Wasser. Eine sehr reiche Molluskenfauna zeigt hier kaum Gezeitenzonierung.

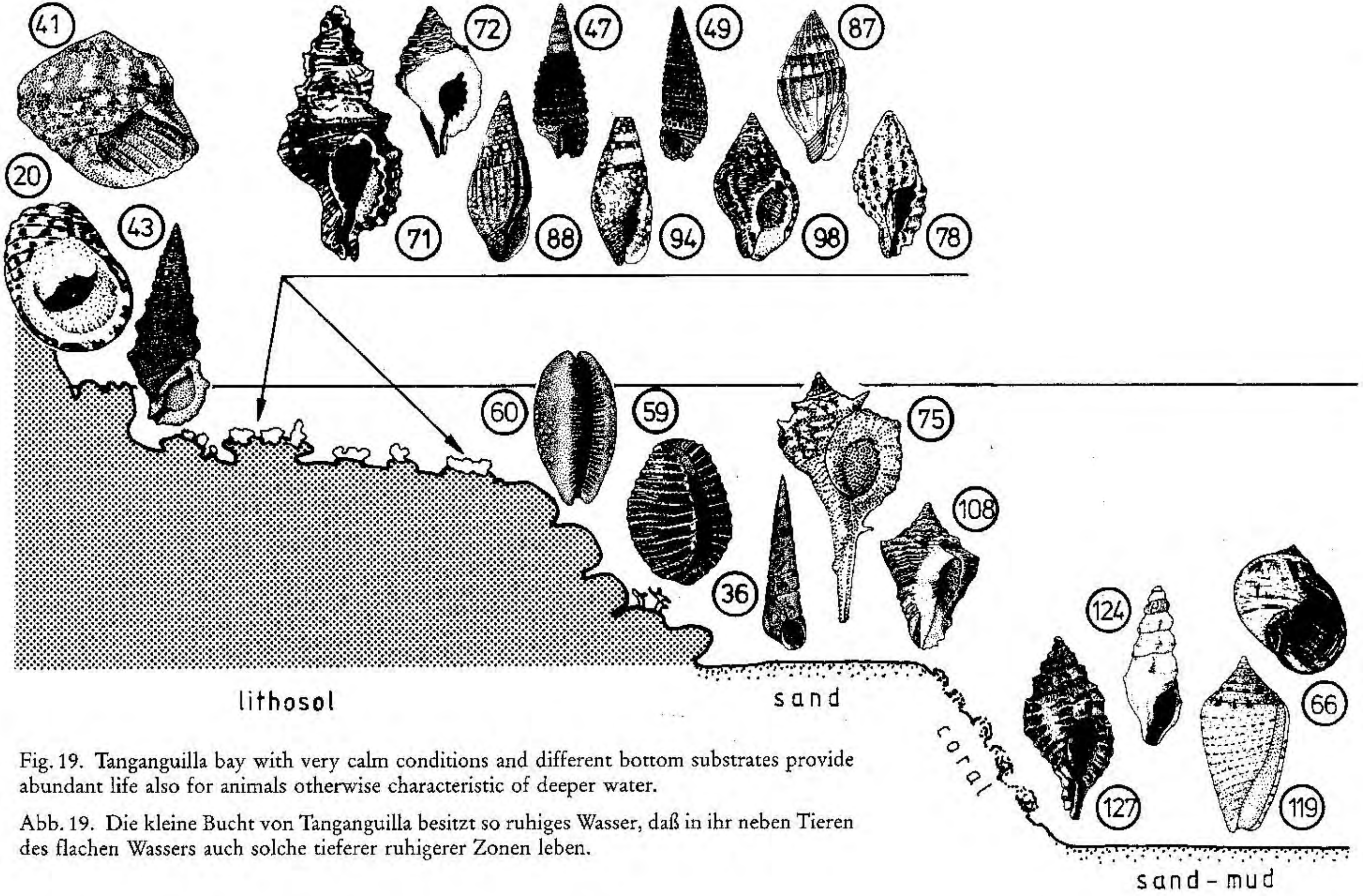


Fig. 19. Tanganguilla bay with very calm conditions and different bottom substrates provide abundant life also for animals otherwise characteristic of deeper water.

Abb. 19. Die kleine Bucht von Tanganguilla besitzt so ruhiges Wasser, daß in ihr neben Tieren des flachen Wassers auch solche tieferer ruhigerer Zonen leben.

C. cinerea, Latirus infundibulum (105), *L. angulatum* (106) and *Fasciolaria tulipa* (107) are present. Among several columbellids the opisthobranchs *Berthellina quadridens, Dendrodoris krebsii, Peltodoris hummelincki igla* and *Chromodoris neona* have been found here.

Taganguilla, a very Calm Bay with Different Types of Substrates.

Taganguilla, a small bay on the eastern side of the peninsula Punta de Betin is separated from the Bahia de Santa Marta by the NW-harbour construction. Water has acces between pillars of this construction, but even strong storms effect the surface of the bay only very little. Currents run evenly and strong and water is always 1°C warmer than in the bay of Santa Marta. Taganguilla village along with large part of the bay of Taganguilla have become filled up during the course of harbour enlargement.

A rich marine life is found in the bay from the shore to the muddy depth (Fig. 19). Just below the rocky shore, rubble and rocks are covered by dense algal growths on which *Turbo castanea, Astraea phoebia, Nerita tessellata* (14), *Modulus modulus* (41) and *Cerithium atratum* (43) graze. The characteristic carnivores found here are *Cymatium nicobaricum* (71), and *C. muricinum* (72). Sponges provide food for *Triphora nigrocincta* (49) and *Cerithiopsis emersoni* (47). *Anachis brasiliana* (88), *A. obesa* (87), *Mitrella ocellata* (94), *Pisania auritula* (98), *Morula nodulosa* (78) and *Leucozonia nassa* are found between and below these rocks in the infralittoral fringe.

In deeper portions of the zone covered by milleporans, *Millepora squarrosa* is replaced by *M. complanta* and *M. alcicornis*. The fauna here resemble that described in Fig. 18. *Cypraea cebra* (60) and *Trivia pediculus* (59) are common.

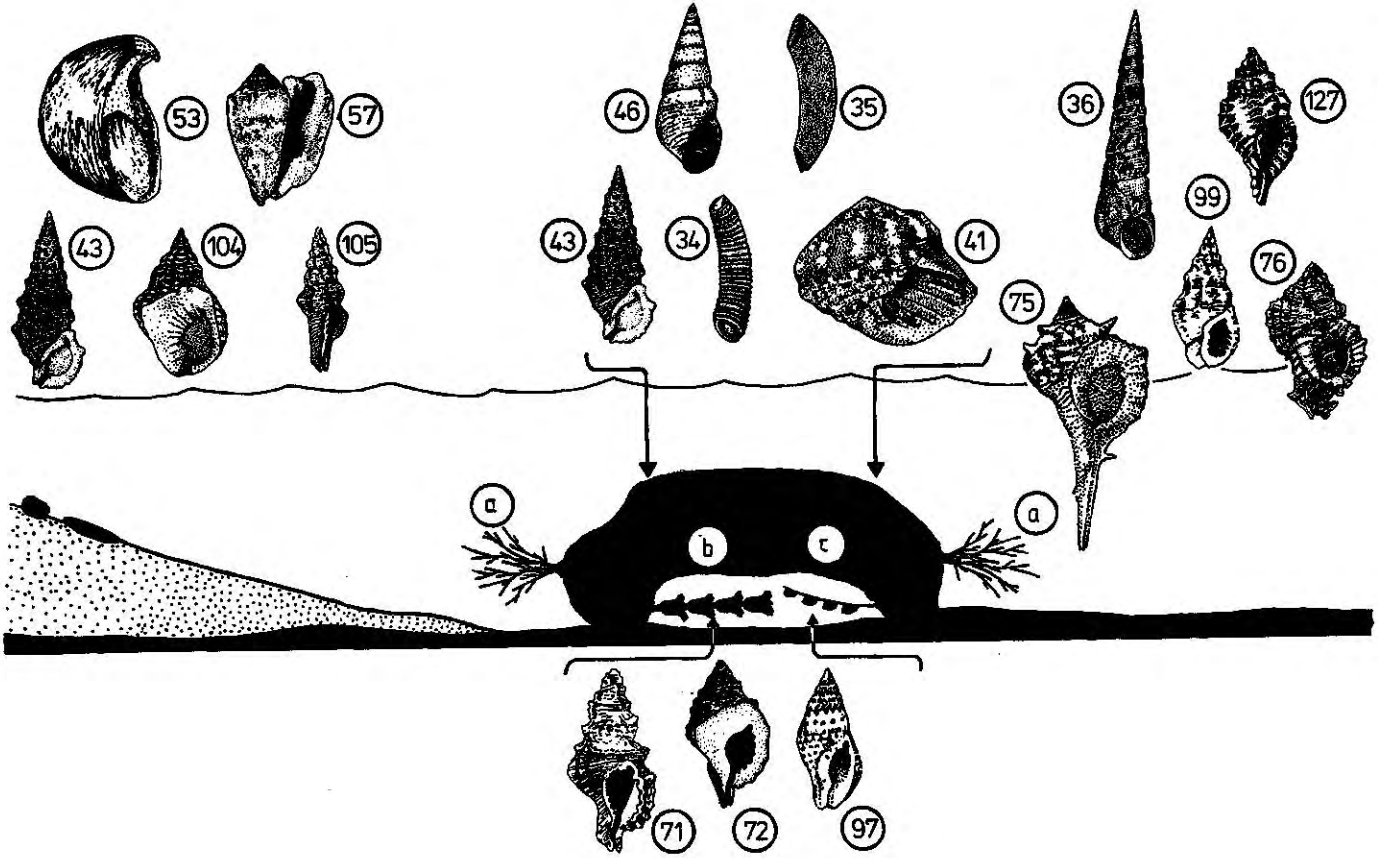
The central part of the bay is covered by soft sediment, with the characteristic *Turritella variegata* (36) hidden within the mud and sand. Hidden within the soft bottom there usually are also *Engoniophos unicinctus, Natica livida, Murex recurvirostris* (75), *Conus jaspideus* and *Vasum muricatum* (108). The *Turritella* community in this bay extends into shallow water of 2 m depth.

Deep hardgrounds and soft bottom in the bay are settled on by *Ocenebra* sp. (127) and numerous turrid species like *Ithycythara* (124) and *Mangelia* but also by *Conus jaspideus* (119), *Xenophora conchyliophora* (55) and *Natica livida* (66). Large hydroids such as *Eudendrium carneum, Cnidoscyphus marginatus* and *Lithocarpus philippinus* are found between corals.

Boulder Resting on Soft Substrate in the Calm Bay of Taganguilla.

The limestone rock lies in 1-2 m depth. The sand to the left continues into the beach (Fig. 20) where *Cerithium atratum* (43), *Latirus infundibulum* (105), *Strombus raninus* (57), *Nassarius vibex* (104), and *Bulla solida* are present. Large conchs of *Cerithium* and *Latirus* may be settled by *Crepidula convexa* (53). Nudibranchs such as *Spurilla neapolitana* and *Dondice occidentalis* are found.

The muddy bottom at the right forms a resting ground for the filter feeding *Turritella variegata* (36), which comes into shallow water in this shallow bay, although it usually occurs at a depth greater than 10 m. *Natica livida, Engoniophos*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unicinctus (99), *Murex recurvirostris* (75), *M. pomum* (76), *Ocenebra* sp. (127), *Conus jaspideus, Vasum muricatum* and *Bulla solida* also live here. The rock is covered by dense growths of algae like *Ulva* and *Enteromorpha* along with others forming tufts and thickets. Here *Caecum pulchellum* (34), *C. nitidum* (35), *Finella dubia* (46), *Cerithium atratum* (43), *Modulus modulus* (41), sometimes also *Turbo castanea* and *Dolabrifera dolabrifera* are found. On the algal tufts also the hydroid *Halecium halecium* (a) is attached.

The lower surface of the rock provides a resting and feeding place for *Cymatium nicobaricum* (71), *C. muricinum* (72), *Pisania pusio* (97) and rarely *C. moritinctum caribbaeum*.

The hydroids *Dynamena conicina* (b) and *Antennella secundaria* (c) are attached to the walls. On hard substrates, lying on the sand or mud, very fine and delicate hydroids of the genera *Clytia, Antennella* are also present as they can survive a certain amount of mud deposition.

Sea-Grass Flats and Sandy Bay — Bahia de Santa Marta.

Sandy beaches and sandy to muddy infralittoral bottom substrate dominate the coast from the Bahia de Santa Marta in a southward direction to the delta of the Rio Magdalena. The Bahia de Santa Marta forms a natural harbour and is protected from the westerly Atlantic current by the Peninsula of Punta de Betin and the two islands Isla de Morrito (Morro Chico) and Isla de Morro (Morro Grande), connected to the peninsula by submerged ridges. Opposite Punta de Betin, on the south and southeast flank of Bahia de Santa Marta, sandy beaches grade into slowly inclined infralittoral sand bottom. The central ship canal is up to 30 m deep and its bottom may be muddy rather than sandy.

The water of the bay and with it that of the harbour is changed continuously by a current that enters the bay parallel to the southern shores, flows along and below the harbour jetties and leaves the bay parallel to the peninsula of Punta de Betin. Here it mixes with a short counter-current (Wedler 1975).

The sandy bottom of the central Bahia de Santa Marta (Banco Pobea) is covered by extended flats of sea-grass (Fig. 21), as are found in all sandy littoral areas of bays to the south and north of Santa Marta. The shallow water of the eel gras flats provides a shelter and a living place for the carnivorous *Polinices lacteus* (63), *Natica canrena* (65), *Murex pomum* (76), *Persicula interruptelineata* (117), *Conus jaspideus* (119) and *Terebra limatula.* Mixed growths of eel-grass and turtle grass often contain large polulations of *Strombus pugilis* (56), and, in addition, less common species such as *Tonna galea, Vasum muricatum* (108), *Turbinella angulata* (109), *Oliva reticulata* (111) and *Prunum prunum* (112). There might not be any trace of these large gastropods as they all periodically hide within the sand or stay in the

◀ Fig. 20. A boulder resting in soft substrate of the calm water of Tanganguilla bay in 1-2 m depth with its molluscan and hydroid fauna.

Abb. 20. Kalkblock in 1-2 m Wassertiefe der Bucht von Taganguilla umgeben von Weichboden mit der Mollusken- und Hydroidenfauna.

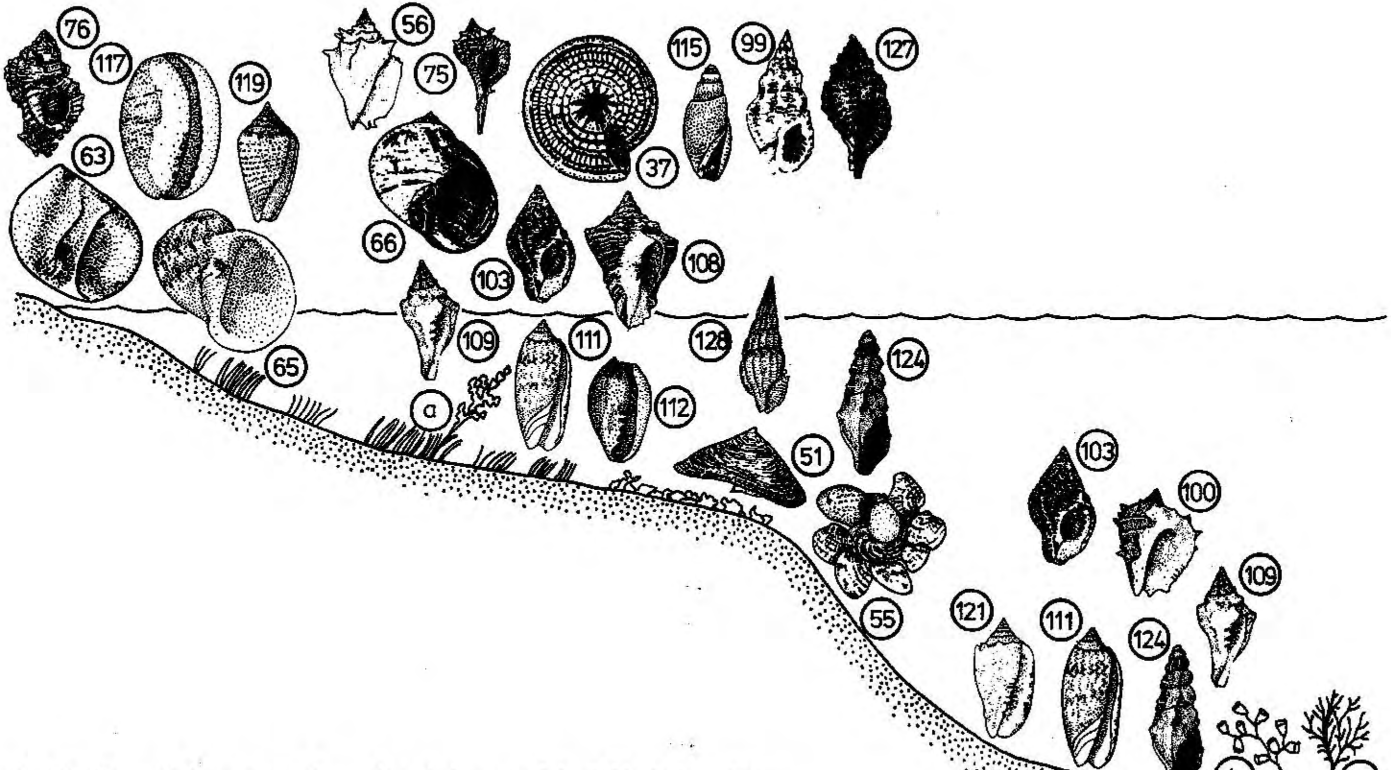


Fig. 21. Fauna of the sea-grass flats and sandy bottom of the Bahia de Santa Marta.

Abb. 21. Fauna der Seegraswiesen und Sandböden der Bucht von Santa Marta.

sand for most of their lives. Smaller gastropods such as *Architectonica nobilis* (37), *Pyramidella dolabrata, Hydatina vesicaria,* some rissoids, *Polinices hepaticus, Natica livida* (66), *Ocenebra* sp. (127), *Murex recurvirostris* (75), *Persicula lavalleana, Olivella perplexa* (115), *O. adelae, Persicula pulcherrima, Engoniophos unicinctus* (99), *Nassarius albus* (103) and *Terebra protexta* are found. During clearwater periods, extended and dense growths of *Ulva* and *Enteromorpha* form on which mass populations of *Aplysia cervina, A. brasiliana* and *Bursatella leachii pleii* often occur and then disappear again at the end of the algal bloom.

The sea-grass flats end at about 15 to 20 m depth.

Secondary hardground of molluscan shells, coral rubble and sponges have developed here. Sponges, coelenterates, bryozoans, tunicates and sedentary polychaetes are present with a hydroid fauna consisting of the species *Eudendrium carneum, Stylactis* sp., *Lovenella gracilis, Halecium bermudense, H. halecium, Cnidiscyphus marginatus, Halopteris diaphana, Antennella secundaria* and *Lytocarpus philippinus.* An extremely rich gastropod-shell fauna can be extracted from this zone. Typical species are *Calyptraea centralis* (51), which is attached to shells of dead bivalves. Different turrids like *Mangelia, Ithycythara* (124), *Drillia, Crassispira* (128) and the well camouflaged *Xenophora conchyliophora* (55) occur, the latter also lives in the more shallow regions of the sea-gras flats. Shells of numerous species of small pyramidellids are present, most of which live on a specific host, commonly a worm-like organism of the infauna of silty and muddy sand. Conids with otherwise rare species like *Conus insularis, C. ermineus, C. largillierti* are present as *Distorsio clathrata. Oliva reticularis* may reach this area, while in more muddy-finegrained sediment *O. caribaea* takes its place.

Near the bottom of the ship canal and in deeper water of neighbouring bays and off the shore to the south of Santa Marta the sediment becomes more fine grained and may be soft mud. *Tonna galea* (70) preys on the irregular sea urchin *Bissus* that forms large populations in the soft bottom. The hydroids *Eudendrium carneum, Halecium muricatum* and *Cnidoscyphus marginatus* are attached to sunken logs, seeds and old coconuts as well as rubble disposed from ships. The gastropods present here are *Calyptraea centralis, Nassarius albus* (103), *Melongena melongena* (100), *Turbinella angulata* (109), *Voluta virescens* (121), *Oliva caribaea* (111), *Ithycythara lanceolata* (124), *Mangelia* dif. spec. and other turrids, many pyramidellids and melanellids.

Sea-Grass.

In the open bays such as Bahia de Santa Marta, eel-grass (*Syringodium filiforme*) dominates in shallow areas, while deeper sands are usually covered by the turtle-grass (*Thalassia testudinum*). Often both grasses form mixed associations (Fig. 22).

A typical gastropod and hydroid fauna is associated with them. *Campanularia columbiana* is the characteristic hydroid on eel-grass (b) and *Halecium dichotomum, Dynamena cornicina* (d), *Sertularia inflata* (f) on turtle-grass. Both grasses are settled by *Clytia edwardsii, Monotheca* (*Plumularia*) *margareta, Plumularia strictocarpa* (a) *Plumularia setacea* and *Obelia geniculata* (c). Colonies of *Myrionema hargitti* (e) are attached on the root system of the grass, while the rocks and larger shells nearby provide a holdfast for *Plumularia halecoides* (g).

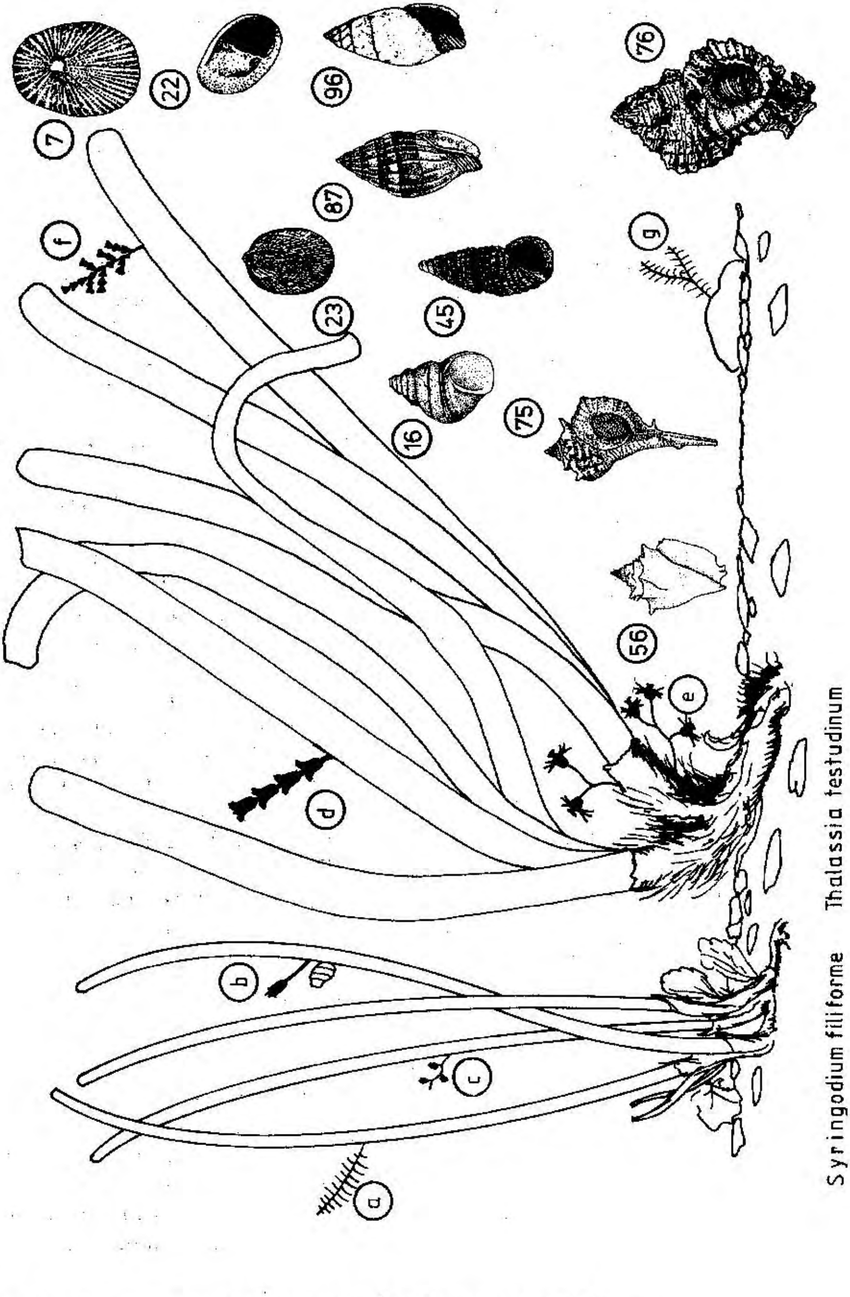


Fig. 22. Sea grass is rooted in the sand and holds a characteristic fauna.

Abb. 22. Seegras ist im Sand verwurzelt und gibt einer ganz eigenen Fauna Heimstätte.

Anachis obesa (87) and *Mitrella lunata* (96) feed on hydroids. *Smaragdia viridis* (22) a small variety of *Collisella* (7), *Phenacolepas hamillei* (23) and *Phyllaplysia engeli* merge with the green colour of the grass or with spots of algae and other epifaunal elements attached to the grass. *Smaragdia* and *Phyllaplysia* even produce green egg masses to merge with the green substrate of the leaves. The small cerithiid *Diastoma varium* (45) is common, while *Alaba incerta* is infrequent. *Tricolia bella* (16) is the trochid of *Thalassia,* while *Tricolia affinis cruenta* is its counterpart on *Syringodium.* Larger gastropods usually encountered near sea grass are *Strombus pugilis* (56) and, less commonly, *Murex pomum* (76) and *M. recurvirostris* (75).

Vagile Substrate: Shell of a Hermit Crab.

Large gastropod conchs provide a substrate for the attachment of the hydroids *Eudendrium carneum, Halecium halecium, Cnidoscyphus marginatus, Halopteris diaphana* and others (Fig. 23). This fauna is also present on gastropod shells that are used as a home for large hermit crabs. Meogastropod limpets are also attached at this place. *Cheilea equestris* and *Crucibulum auricula* (52) settle on large conchs of living gastropods as well as on shells carried around by hermit crabs, *Crepidula plana* (54) is attached to the inner lip of the aperture only in conchs carried by hermit crabs.

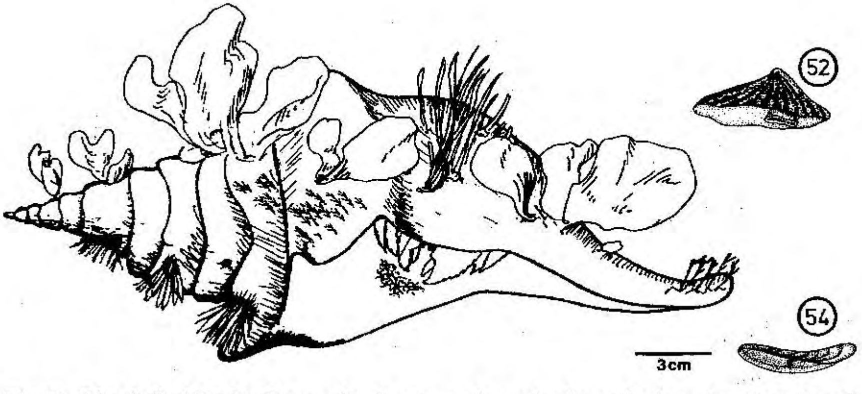
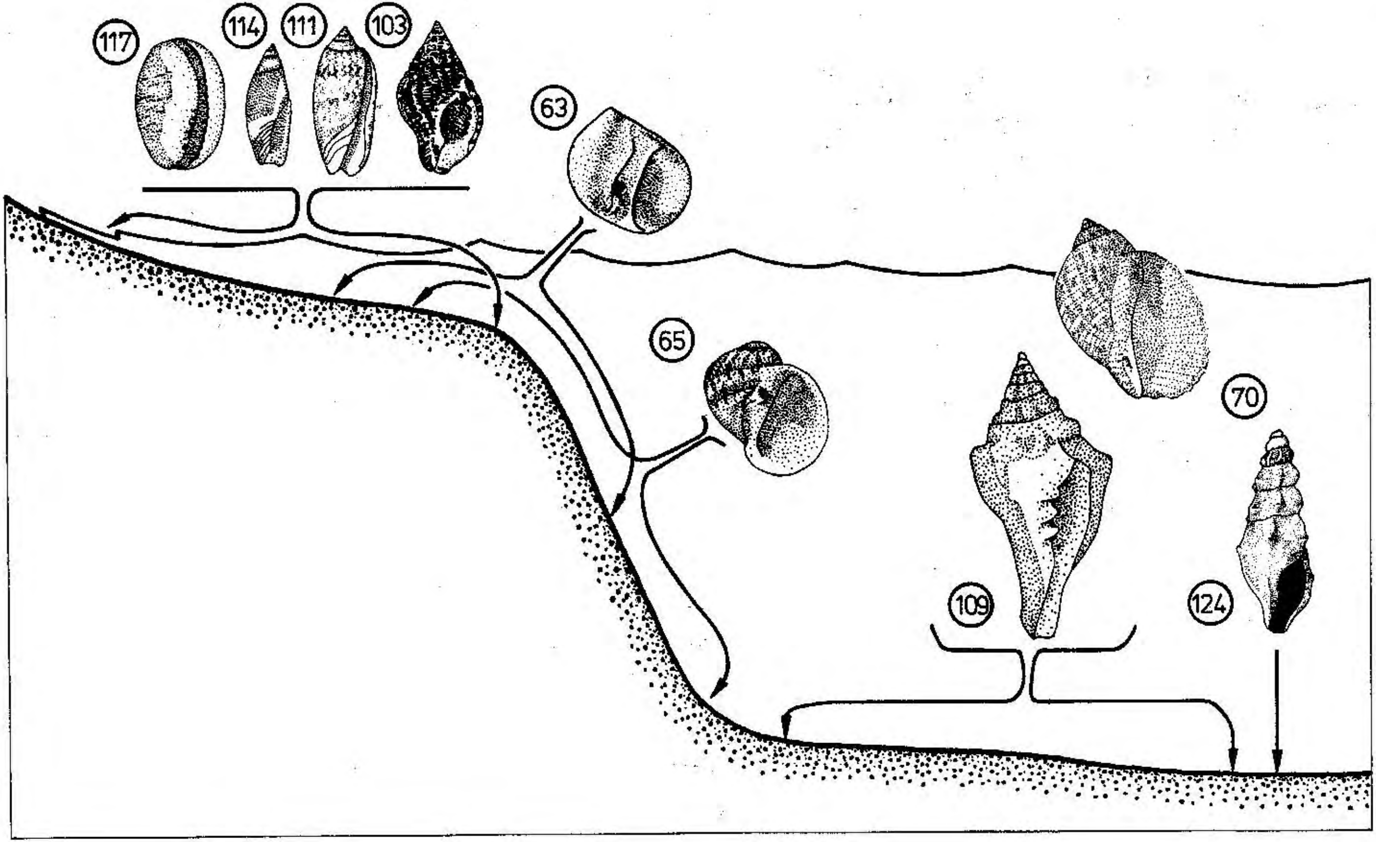


Fig. 23. The shell of *Turbinella angulata* is commonly used as home for large hermit crabs and is settled by epibenthos.

Abb. 23. Das Gehäuse von *Turbinella angulata* wird von großen Einsiedlerkrebsen gern genutzt und ist von Epibenthos besiedelt.

Sandy Beach of the Ensenada de Concha.

At the portion of the Ensenada de Concha (Fig. 1, loc. 4; Fig. 24) beaches are protected from the swell of the open sea for most of the year. The shore drops off rapidly on the east side of the beach and declines evenly on western side. The sand bottom below low tide line, and above the beginning of the sea-grass flat on the evenly inclined slope is densely settled on by sanddollars (*Mellita lota* and others)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upon which the large *Cassis madagascariensis* and *C. tuberosa* prey. *Polinices lacteus*, *Ocenebra* sp., and *Conus jaspideus* are present here as well.

The sea-grass in 2-5 m depth supports a large population of *Strombus pugilis* and some *Vasum muricatum* and *Turbinella angulata* and a rare *Xenophora conchyliophora*. The grass shows the typical hydroid and gastropod associations as described in Fig. 22.

Within the more muddy sand below 5 m depth with scattered growths of sea-grass *Polinices hepaticus*, *Natica livida*, *Nassarius albus*, *Aesopus stearnsii*, *Oliva reticularis*, *Olivella adelae*, *Persicula punctostriata*, *Olivella perplexa*, *O. petiolita*, *Conus jaspideus*, *C. spurius*, *Crassispira* sp., *Mangelia* dif. spec. and *Ithycythara lanceolata* are found.

The eastern side of the head of the Ensenada de Concha shows a rapid drop from the shore to 15-20 m depth and from sand to calcareous mud. Mainly the activity of endobenthic crabs produced strong bioturbation and a pitted bottom surface. The only conspicuous benthic animals here are long sea whips (gorgonians). Apart from a few large *Turbinella angulata* (109) and *Tonna galea* (27) the mud bears numerous small turrids, among them *Mangelia conica* and *Ithycythara lanceolata* (124).

The beach above consists of well sorted coarse sand. Agile hunters such as *Oliva reticularis* (111), *Persicula interruptelineata* (117), *Olivella nivea* (114) and *Nassarius albus* (103) roam the infralittoral fringe. The snails may leave the sand only to get hold of some prey, they otherwise remain within the sand and, with the exception of *Nassarius*, also move within the sand. The rippled finer sand near the edge of the steep slope, in addition, contains *Polinices lacteus* (63), *Natica canrena* (65) and *Aesopus stearnsii*. Only *Natica canrena* enters also the instable sand of the steep slope which is otherwise free of living gastropods.

Pebble Beach Protected by Patch Reef.

The opposite side of the eastern end of the Ensenada de Concha which also drops rapidly to the deep muddy floor, consists mainly of hard substrates with a small submerged terrace. The beach is formed by slabs of metamorphic rock and coral rubble piled into a roof-tile-pattern by the waves. Spaces between and below pebbles remain open and are continuously washed by currents generated by the waves. The shingle pattern continues into a shallow lagoon that is less than 1.5 m deep and protected from the bay by a patch reef that breaks the waves but is continuously awash (Fig. 25). This gravel-rubble bottom supports an extremely rich gastropod and chiton fauna of more than 60 species.

Seven gastropod zones can be distinguished in the gravel beach. Zone 1 lies about 10 to 15 cm above water line and is settled by scattered individuals of *Nerita fulgurans* (18) and *Planaxis nucleus* (40). This zone is about 20 cm wide.

◀ Fig. 24. Sandy beach of the Ensenada de Concha with its steep drop-off to muddy bottom with fauna of the beach, the unstable slope and the muddy, strongly bioturbated flat bay bottom.

Abb. 24. Profil in der Bucht von Concha mit typischer Sandstrandbesiedlung und steilem Sandhang zum kräftig durchwühlten, schlammigen, ebenen Buchtboden.

Zone 2 measures about 20 cm in width and ends at the water line. *Nerita fulgurans* and *Planaxis nucleus* are the dominant gastropods here, but *Nerita tessellata* (14), *Planaxis lineatus* (39) and *Littorina meleagris* (28) are also present.

Zone 3 reaches a depth of 6 cm. Here *Nerita tessellata* dominates and *Littorina meleagris, Planaxis nucleus* and *P. lineatus* are common. *Phidiana lynceus,* small individuals of *Nitidella ocellata* (92), *Nerita fulgurans* and small individuals of *Acmaea* and *Collicella* (7) are present.

Zone 4 measures about 35 cm in width and reaches from 6-12 cm depth. Here *Nerita tessellata* and *Littorina meleagris* dominate. *Tegula excavata* (10) and *Collisella antillarum* (7) are common. Here, as in zone 3 and 5, hard substrates are covered with the white cupolae of egg capsules of species of the genus *Nerita.* Some individuals of *Planaxix lineatus, P. nucleus, Mitrella ocellata* (94), *Chiton tubercularis* (1) and *Stenoplax limaciformis* are present.

Zone 5 is 40 cm wide and 16 cm deep. The dominating fauna are *Collisella antillarum,* small individuals of *Chiton tuberculatus* and *Nerita tessellata. Littorina meleagris, Tegula excavata* and *T. viridula* (9) are commonly found. Besides these, *Phidiana lynceus, Nitidella laevigata* (93), *Aplysia cervina, Nerita fulgurans* and *Morula nodulosa* (78) are present.

Zone 6 is 80 cm wide and reaches down to 22 cm depth. Individuals of *Collisella antillarum* are once again present in large numbers. Common are *Nitidella nitida* (92), *Chiton tuberculatus* and *Acmaea pustulata.* Small attached bivalves like *Chama* and *Isognomon* are common. *Phidiana lynceus, Ischnochiton limaciformis* and small individuals of *Fissurella* are present.

Zone 7 lies below 22 cm depth and occupies the gravel area between the beach zones 1-6 and a small patch reef composed of the branching coral *Porites.* Water continuously streams through this small lagoon which is well protected from the force of waves and strong currents. Below and on the rocks there is a maximum diversity of species. The following chitons are present: *Stenoplax limaciformis, Ischnochiton pectinatus, I. papillosus, Lepidopleurus pergranatus, Lepidochitona liozonis, Chiton tuberculatus, Acanthochitona pygmaea.* Archaeogastropod limpets are found with *Lucapinella limatula, Lucapina suffusa, Hemitoma octoradiata* (6), *Fissurella angusta* (4), *Diodora listeri* (3), *D. variegata, Acmaea pustulata* and *Collisella antillarum.* Mesogastropod limpets are represented by *Cheilea equestris* and *Hipponix antiquatus* (50). Archaeogastropods with a trochospiral shell are present with *Calliostoma sarcodum, Tegula viridula, Astraea caelata* (13), *Arene tricarinata, A. cruentata.* The herbivorous mesogastropods are represented only by *Cerithium atratum* (43) and *Diastoma varia* (45). Carnivorous mesogastropods such as *Trivia pediculus* (59), *Bursa granularis cubaniana* (73), *Cymatium nicobaricum* (71), and *C. pileare* are found. Neogastropods predominate in the number of species. *Ocenebra rosea* (79), *Morula nodulosa, Thais rustica* (83), *Murex brevifrons* (77), *Aspella paupercula, Favartia alveata* and *F. cellulosa* represent the muricids; *Anachis brasiliana* (88), *A. sparsa* (90), *A. obesa* (87), *A.* div. spec, *Nitidella nitida, Mitrella lunata* (96) represent the columbellids; *Pisania pusio* (97), *P. auritula* (98), *Engina turbinella, Leucozonia nassa* (101) represent buccinids and fascioloriids, *Hyalina avena* (116), *H.* sp., *Vexillum puella* (110), *V. dermestinum, V. hendersoni* represent volutids and mitrids; and turrids are badly represented; *Crassispira albumaculata* is the only species found.

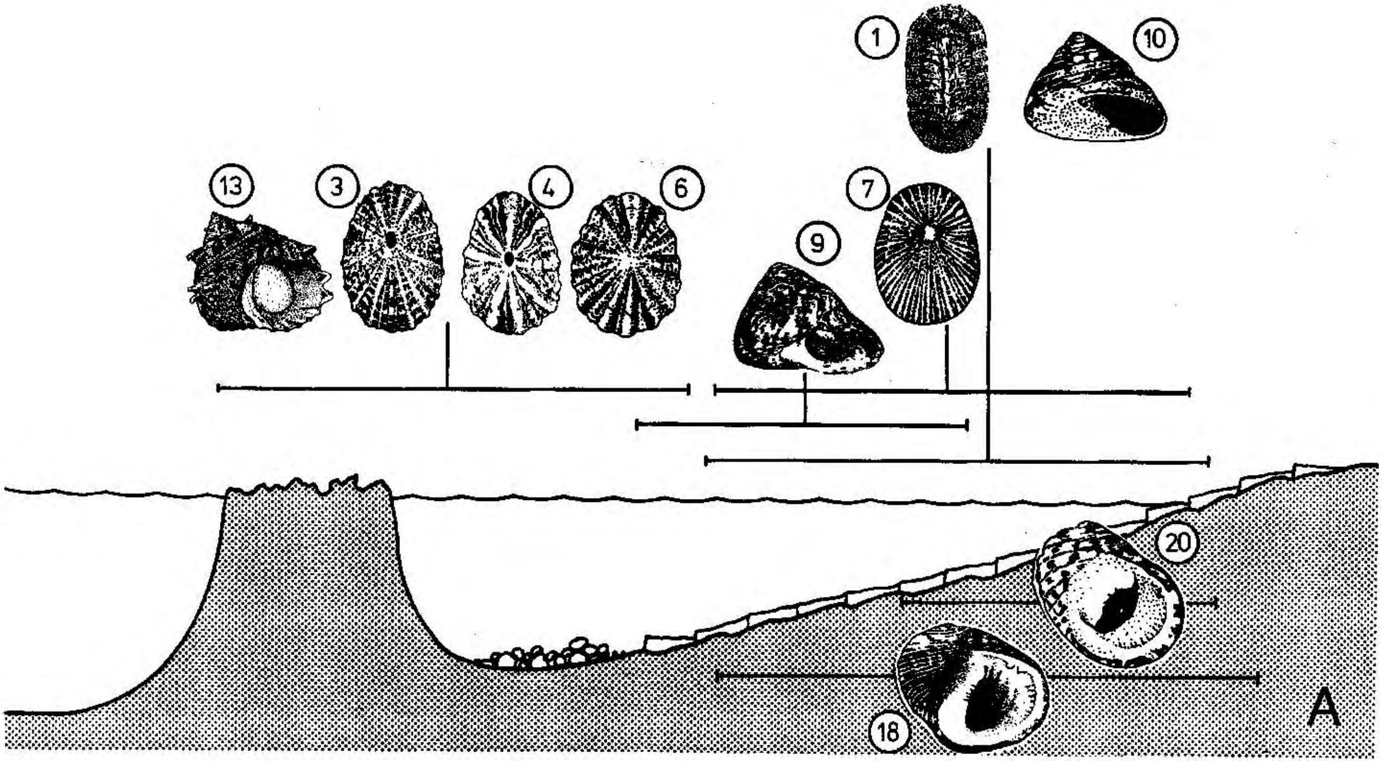
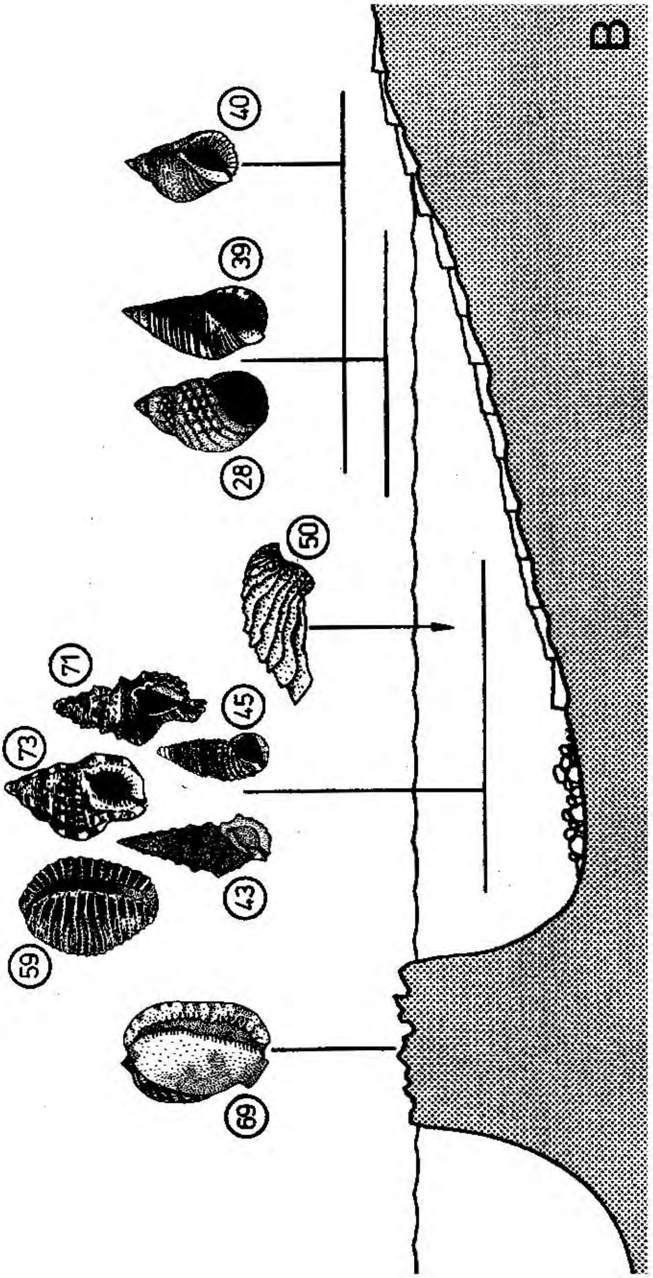


Fig. 25. A-C. A pebble beach that is protected by a patch reef in the Ensenada de Concha provides living environment for an extremely rich molluscan fauna.

Abb. 25. A-C. Ein durch ein „patch reef" geschützter Geröllstrand in der Ensenada de Concha bietet Lebensraum für eine äußerst reiche Mollusken-Fauna.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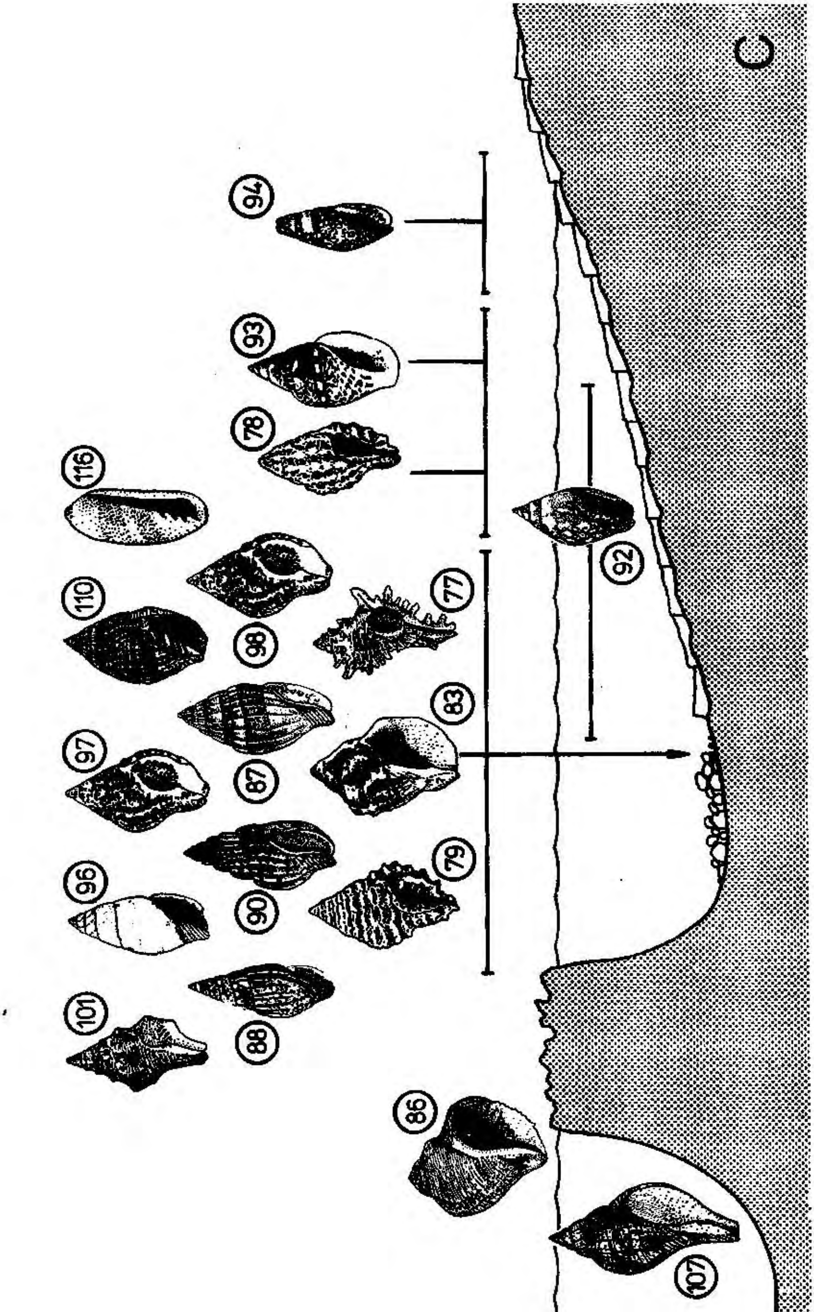
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The patch reef bordering this lagoon teams with gastropod life and *Coralliophila abbreviata* (86), *C. aberrans* and *Peltodoris hummelincki igla* have settled on it. The sand and rubble below the reef contains *Cypraecassis testiculus* (69), *Cymatium moritinctum caribbaeum, C. pileare, Ocenebra rosea, Murex brevifrons, Engina turbinella* and *Fasciolaria tulipa* (107).

Between the base of the patch reef in 1.5 m depth and corals growing at 3 m depth, a weakly inclined terrace has developed, covered with calcareous sand and rubble. In algal thickets covering this substrate numerous microvorous gastropods such as members of the genera *Caecum, Diastoma, Alaba,* are present along with different rissoids, turrids and volutids. The sand is populated by turrids as well as by representatives of *Natica* and *Polinices.* Below this sandy platform, the slope is strongly inclined and densely covered by living corals and *Gorgonia.* Here a fauna is found as has been described from the rocky shore near Punta de Betin (Fig. 10) and the off shore slope of the coral reef from Ensenada de Chengue (Fig. 30).

Sand Beach with Fresh Water Discharging through it — Bahia Nenguangue.

The beach of the headwater of the Bahia Nenguangue (Fig. 1, loc. 1) consists of well sorted sand up to about 1 m depth, succeeded by a pebble zone and then once more by sand (Fig. 26). The beach bar pools up the little creek Santigos and the pools holds a rich population of *Assiminea* sp. (33). Creek water seeps through the sand and organic material coming with it is exploited by worms. These are in turn the food of *Terebra cinerea* (122). As the tides come in or recede, the *Terebra* moves up and down the beach, remaining in a zone in which they benefit from the breaking waves for a maximal length of time. When a wave travels shorewards, *Terebra* issues from the sand, allows itself to be carried by the water until the force of the wave slackens, then hastily digs into the sand again. Up to 10 animals were noted in one meter square of the beach.

The sandy bottom of the sublittoral beyond the pebble zone of the infralittoral fringe is roamed by *Polinices lacteus* (63) and *Prunum prunum* (112).

Sandy Shore with Sublittoral Fresh Water Emergence — Ensenada de Taganga.

In front of the village of Taganga (Fig. 1, loc. 6) fishermen land, clean an sell their fish. On calm days *Nassarius vibex* (104) uses this carion even within the intertidal zone. Among rocks in the sand in the infralittoral fringe *Cymatium pileare, Latirus infundibulum* (105) and *Murex brevifrons* (77) are common. The hydroids *Halocordyle disticha* (a) and *Halecium halecium* (b) are present here. In the sand on the beach *Polinices lacteus* and *Oliva reticularis* are found. The slope down to about 4 m of depth is covered with a muddy substrate at calm times from which a dense thicket of green algae arises (Fig. 27). A fauna with many individuals of *Cerithium atratum, Bulla solida,* div. spec. of *Caecum, Diastoma varium, Alaba incerta, Finella dubia, Cylichnella bidentata, Tornatina candei* and several rissoids, *Anachis obesa* and *Mitrella lunata* is present here.

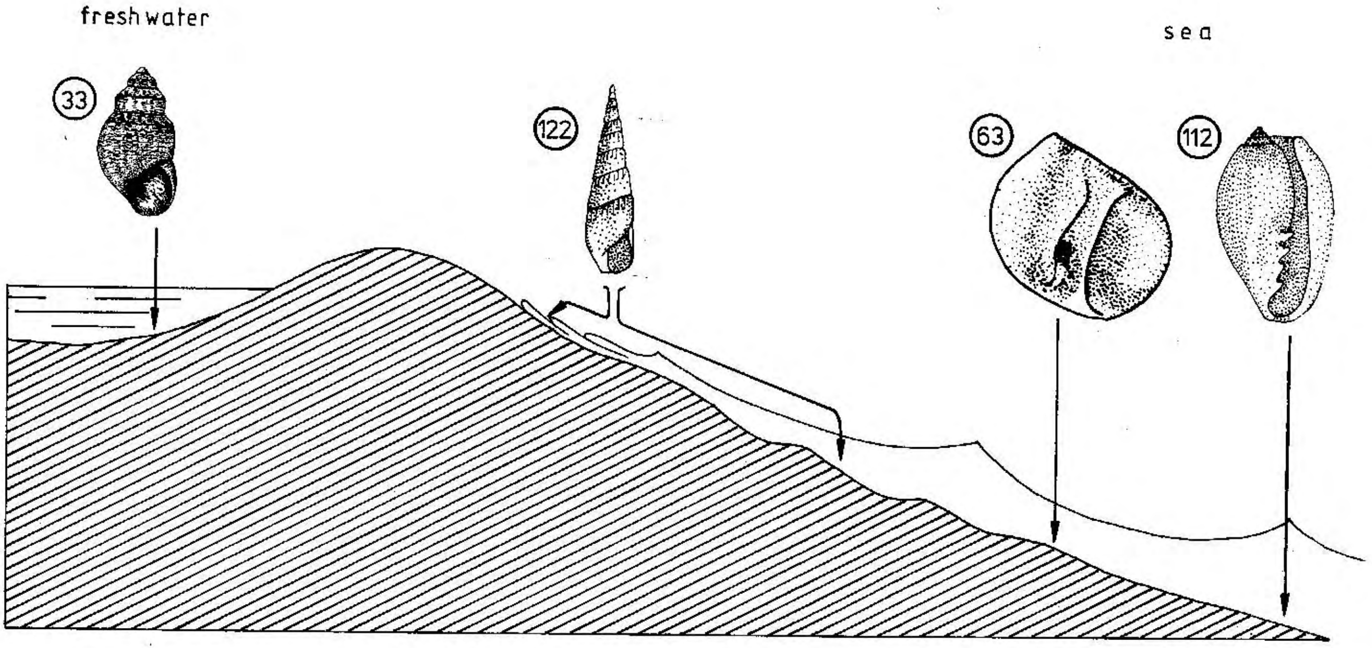


Fig. 26. Fresh water discharges through the sand beach of Bahia Nenguangue. Here, those worms that are hunted by *Terebra cinera* (122), find a suitable living environment.

Abb. 26. Süßwasser sickert durch den Sandstrand der Bucht von Neguangue, und damit fühlen sich hier Würmer wohl, die von *Terebra cinera* (122) im Sand des Gezeitenbereiches erbeutet werden.

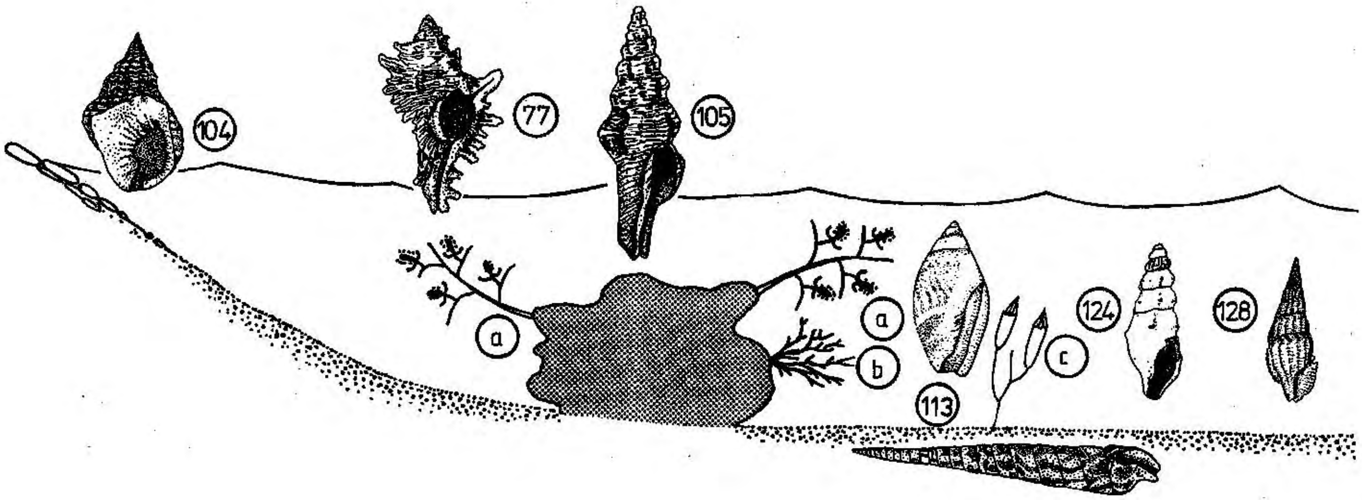


Fig. 27. Fresh water discharges in the sublittoral sand of the Ensenada Taganga supporting an infaunal life that is utilized by a number of carnivorous gastropods. Surrounding areas are those of the sandy and muddy bay bottom.

Abb. 27. Süßwasser tritt im Sand der Bucht von Taganga unterhalb des Niedrigwassers aus. Hier lebt eine reiche Bodenfauna, die von einer Anzahl von Neogastropoden erbeutet wird. Die Umgebung wird durch Sand und Schlickboden mit Seegras und typischer Fauna gekennzeichnet.

At least 3 different species of living pyramidellids were extracted from the sandy substrate.

In about 2-4 m deep water, the bottom is not covered by sea grass due to water turbidity and to ground water issuing through the sand. A rich fauna of gastropods in search of infaunal life is present here, the most conspicuous of which is *Terebra taurinus.* Up to 10 of the large *T. taurinus* may be found in one square meter of bottom, each half or fully hidden in the muddy sand at the end of a clearly visible trail. *T. taurinus* is extremely rare on other sandy bottoms. The hydroids *Calicella gabiella* (c) and *Lovenella gracilis* are attached to the shell of *T. taurinus.* Apart from *T. taurinus* several other species of *Terebra,* and several species of turrids of the type *Crassispira* (128), *Ithycythara* (124), and *Mangelia* are present.

In deeper water at about 7 m depth, sea grass covers the sand. A rich population of *Strombus pugilis* is accompanied by *Ocenebra* sp., *Polinices hepaticus, Murex recurvirostris, Olivella adelae, Terebra dislocata,* several species of *Mangelia, Crassispira* sp. and *Ithycythara lamellosa.* Algae and sea grass are settled on by *Caecum* and *Finella,* and pyramidellids live in the sand.

Beach rock — Punta la Loma.

An outcrop of rock lying on a sandy beach (Fig. 1, loc. 12), like in Punta Brava (see Fig. 29) consists of a calcareous beach rock platform that extends for 50 m from the upper intertidal zone in seaward direction and then ends abruptly. Brackish water may reach this area periodically; turbidity and the burden of suspended material is increased. The beach rock (limestone) contains pools and is interrupted by deep fissures with a bottom of sand and rubble (Fig. 28). The algal flora is quite similar to that of the Punta Brava. Green algae such as *Ulva rigida, Enteromorpha* sp., *Caulerpa mexicana, C. sertularioides* and *Codium isthmocladum,* brown algae like *Spatoglossum schroederi, Dictyopteris delicatula* and *Sargassum vulgare,* and red algae such as *Pseudogloiophloea halliae, Halymenia* sp., *Grateloupia filicina, Solieria tenera, Gracilaria foliifera, Vidalia obtusiloba, Bryothamnion seafothii* and *Batrylocladia shanksei* grow here and form extensive covers on the rocks.

In the upper intertidal zone, *Conus mus* (118) is found, often buried into wet sand at low tide, where the beach rock dips below the sand of the beach. *Tegula lividomaculata* (11) is characteristic of the intertidal zone and the infralittoral fringe. Its conchs are often settled on by *Crepidula convexa* (53). *Leucozonia nassa* (101), *Morula nodulosa* (78), *Thais haemastoma* (81) and *Pisania auritula* (98) are found on the whole platform. Below rocks and gravel *Ischnochiton striolatus, Aspella paupercula* and *Dendrodoris krebsii* are present. Of the columbellids *Anachis sparsa* (90) and *A. brasiliana* (88) are found on and below rocks, while *Nitidella laevigata* (93) and *Columbella mercatoria* (91) dwell and feed on algae. In algal tufts *Tricolia affinis* (15) and *Tricolia tessellata* (14) are present. *Fasciolaria tulipa* (107) feeds on the rich community of gastropod of the platform. The only hydroids found here are those that settle on algae, such as those found at Punta Brava.

Granitic Boulders in Exposed Sand Beach — Punta Brava.

Some granite boulders are found on the sandy beach at the airport Simon Bolivar of Santa Marta (Fig. 1, loc. 13). The waves washing the boulders scourge them with

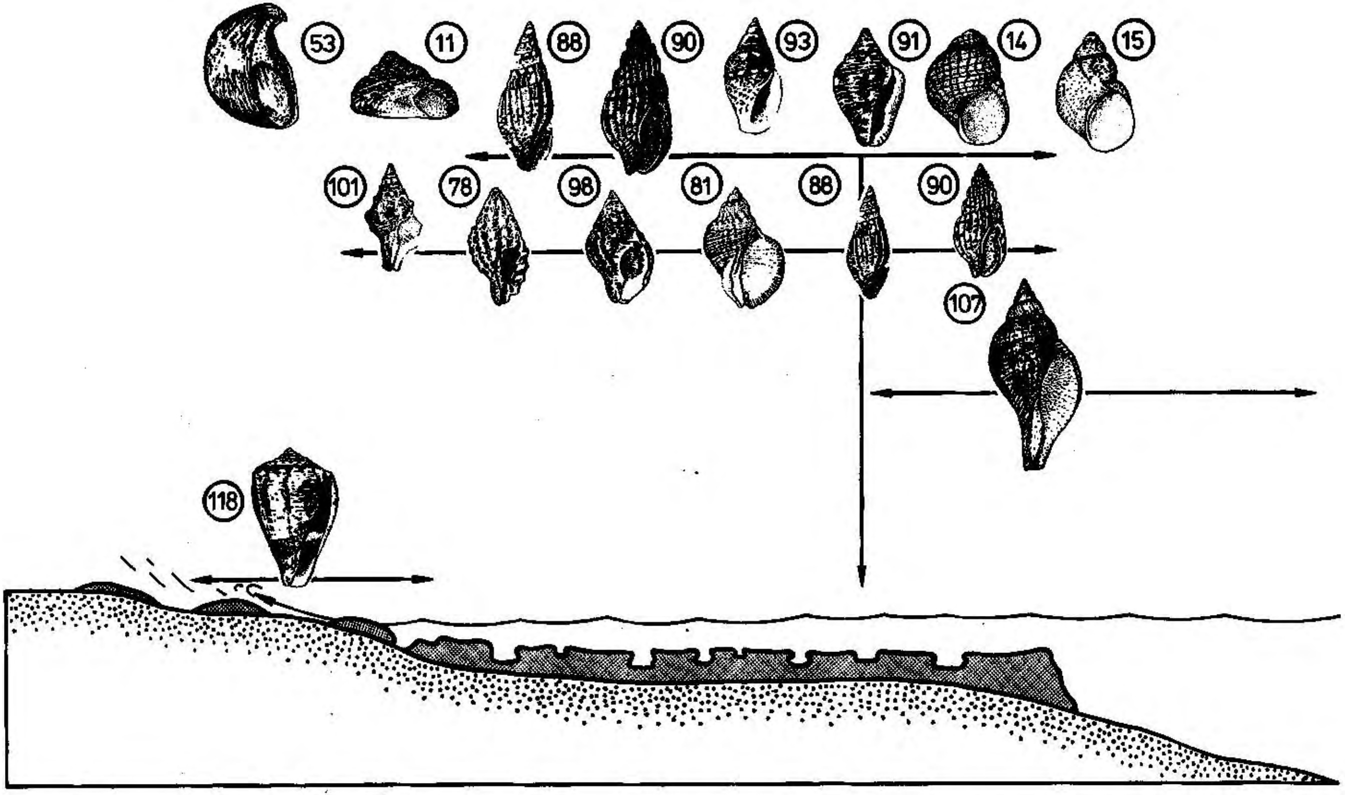


Fig. 28. The beach-rock outcrop at Punta La Loma provides hard substrate surrounded by extensive sand bottom. It is settled by dense algal growth and a characteristic molluscan and hydroid population.

Abb. 28. Zementierter Kalksand von Punta La Loma wird von lockerem Sandstrand und Sandboden umgeben und ist von reichem Pflanzen- und Tierleben bedeckt.

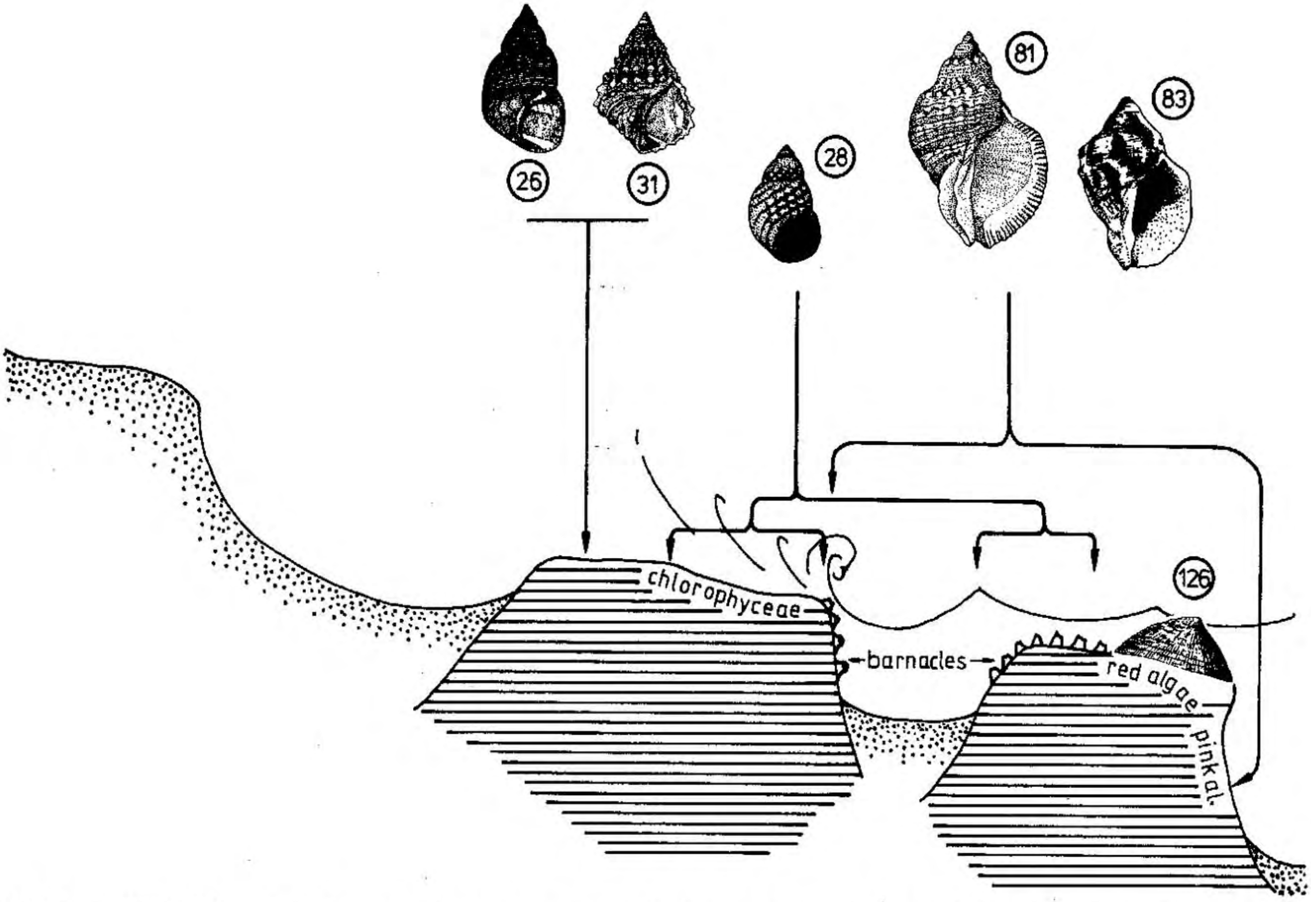


Fig. 29. The granitic boulders of Punta Brava, like the beach rook of Punta La Loma, are surrounded by sand. But, the fauna is considerably different.

Abb. 29. Granitblöcke von Punta Brava sind ebenso von Sand umgeben wie die Strandzementplattform von Punta La Loma, doch ist ihre Besiedlung ziemlich verschieden.

sand caught up in the sea. Brackish water comes periodically from the Cienaga Grande and the mouth of the Rio Magdalena, increasing turbidity of the water (Fig. 29).

The uppermost light green algal zone with *Ulva, Enteromorpha, Caulerpa* and *Codium* on the boulders remains wet due to the splash of the waves. On the top of boulders *Nodilittorina interrupta* (31) and *Littorina meleagris* (28) and a few *Nodilittorina ziczac* (26) form mixed populations. The intertidal zone with brown algae such as *Spatoglossum, Sargassum* and *Dictyopteris* supports *Littorina meleagris* populations that feed on the rocks down to the pink crust of calcareous algae. The limpets *Fissurella nimbosa* and *Siphonaria pectinata* (126) live within the zone of brown and red algae found between a barnacle zone and above the pink zone with crust forming calcareous algae. While *F. nimbosa* penetrates the barnacle zone, *S. pectinata* remains below. Limpets and barnacles are preyed upon by *Thais rustica* (83) and *T. haemastoma* (81).

The most conspicuous hydroid here is *Thrycoscyphus ramosus*, which forms up to 20 cm long colonies in the shaded and current swept channels between boulders, supporting a rich population of holothurians. Other hydroids settle on the solid thalli of the Phaeophyta, like: *Campanularia lennoxensis, Dynamena quadridentata, Aglaophenia latecarinata, Clytia simplex, Diphasia tropica* and *Plumularia strictocarpa.*

Bay with Coral Reefs and Lagoons — Ensenada de Chengue.

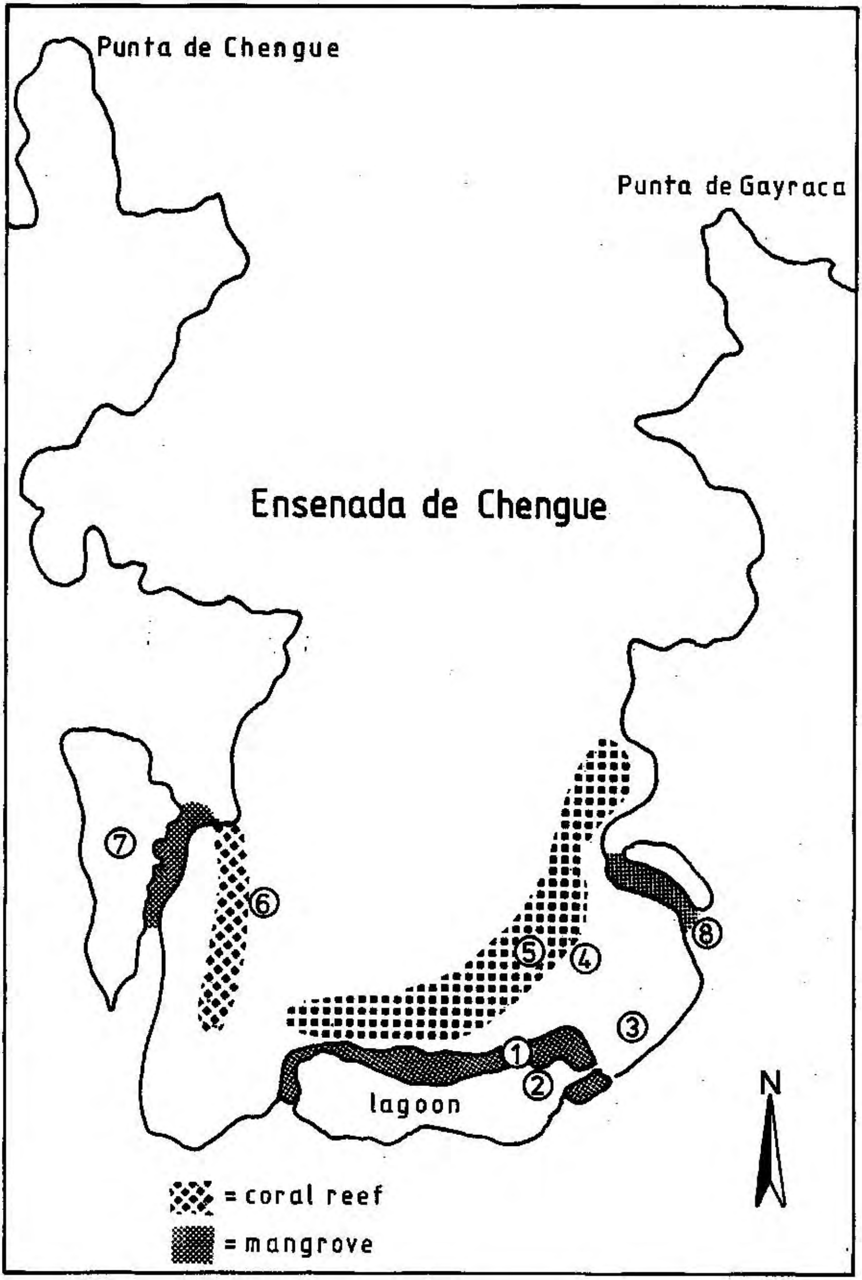
This large bay in the NE of Santa Marta (Fig. 1, loc. 1) is bordered by steep rock cliffs on both sides rising into mountain chains of the Sierra Nevada. The mouth of the bay opens toward the North. With the exception of a smaller westerly side-bay, the shores of the Chengue bay are protected from the main swell of the open Caribbean Sea by rocky cliffs of the Punta de Gayraca. At its southern end, the bay becomes more shallow until the floor slowly rises above sea level where a fringe of mangrove forrests borders three small lagoons. Coral reefs grow in the southern extentions of the bay and, with exception of the easterly one, are accompanied by shallow back-reef lagoons (Fig. 30).

The central and easterly coral growths mainly consist of *Acropora palmata* thickets (Fig. 30: 5) and in the deeper region of *Agaricia* sp. During brisa time, when the currents in the bay are weak and the water is clear, up to 7 m, usually approx.

Fig. 30. Map of the Ensenada Chengue. — 1. Mangrove — coral rubble ridge (Fig. 31). 2. Mangrove lagoon with narrow, small inlet (Fig. 31). 3. Coral-reef lagoon influenced by salinal lagoonal water. 4. Coral-patch reefs. 5. Coral reefs and *Acropora* thickets. 6. Chengue coral reef (Fig. 33). 7. Salt lagoon. 8. Mangrove with prop roots (Fig. 32). ▶

Abb. 30. Karte der Bucht von Chengue. — 1. Mangrovenbestandener Strandwall aus Riffschutt (Abb. 31). 2. Lagune mit erhöhtem Salzgehalt und schmalem Einlaß (Abb. 31). 3. Riff-Lagune, von Salzwasser der Mangrove-Lagune beeinflußt. 4. Korallen – Fleckenriffe. 5. *Acropora*-Dickicht und Korallenriff. 6. Chengue-Korallenriff (Abb. 33). 7. Salz-Lagune. 8. Mangrove, die Luftwurzeln in die Lagune schickt (Abb. 32).

4 m long *Sargassum* bushes grow on large boulders of this area. On them huge populations of *Alaba incerta* develop within a short time. Other common gas-



tropods on these algae are *Tricolia affinis, Diastoma varia, Mitrella lunata* and *Stylocheilus longicauda.* After brisa season, during rainy periods, swell coming from the N or NW may enter the bay and detach *Sargassum* from its anchorage, which then drifts off or is washed to the beaches. Shells of gastropods that live on *Sargassum* are thus found mixed with those of gastropods associated with coral thickets, like members of the genera *Cypraea, Triphora, Cerithiopsis* and *Coralliophila,* or with those typical of sandy bottoms such as *Olivella, Oliva, Nassarius, Terebra,* turrids and pyramidellids.

The bottom on the seaward easterly side-bays of the Ensenada de Chengue is formed by calcareous sand with patches of *Acropora* and coral heads of hemispheroidal shape scattered throughout. In well sorted sand, *Conus regius, Nassarius albus, Cypraecassis testiculus* and members of the genus *Olivella* are common. The sandy beach just above supratidal zone is used by sea turtles to deposite their eggs. The sand just below the intertidal zone of the westerly bays is well sorted and rippled. In this continuously shifting sand only species of *Oliva reticularis, Persicula punctostriata, Nassarius albus* and *Polinices lacteus* are found in depths of up to 3-5 m. After this point, sea grass stabilizes the bottom. The bay wall on the eastern side may drop stepply at some places to great depth of over 40 m. Corals growing on the slope are dominated by *Agaricia agaricites.* Shore debris nearby consists of large coral fragments. Here *Nerita tessellata* and *Littorina meleagris* are found within the intertidal zone. The lower side of large slabs or coral limestone found just below the tidal line, are often covered by small stony corals on which *Coralliophila aberrans* feeds.

Thickets of *Acropora* found in deeper portions at the end of the bay form a special environment (Fig. 30: 5). Juveniles of a number of gastropods such as *Strombus gigas* find shelter here. Sponges encrusting dead portions of coral colonies are settled on by *Seila adamsi,* different species of the genera *Cerithiopsis* and *Triphora* and *Emarginula pumila.* The sand between *Acropora cervicornis* colonies and outside of the thickets provides living environment for large gastropods such as *Tonna galea, Vasum muricatum, Strombus gigas, Phalium granulatum* and *Strombus raninus.* Smaller species like *Natica canrena, Engoniophos unicinctus, Nassarius albus, Conus jaspideus* and *Crassipira* sp. hunt for food here.

Often the bottom is covered with a light algal tuft consisting of entangled filamentous green algae (Fig. 30: 3). Here *Diastoma varia,* different species of *Caecum, Bulla striata* and *Tricolia bella* make use of the plants, while *Anachis obesa, Mitrella lunata, Pyramidella dolabrata, Persicula lavalleana* and *Olivella perplexa* hunt the animals living in the shelter of the tufts. When muddy and sandy substrates in depths less than 1 m are covered with such algal tufts (for example in the protected northern portion of Ensenada de Cinto), the fauna is very similar and only *Persicula pulcherrima* and rissoids are new.

A broad ridge crosses from the eastern cliffs to the head of the bay. It used to be a reef with a large back-reef lagoon behind it. Now the easterly part consists of a few living corals and thickets of *Acropora* with a lot of coral rubble and calcareous sand between them. The structure of this coral reef is closely associated with the formation of the lagoon of the Salinas de Chengue (Fig. 30: 2). Not long ago, this lagoon was open and shallow lying behind a fringing reef. When stroms piled up a gravel ridge on the corals the lagoon became closed off and restricted current conditions developed.

Closed Lagoon and Mangrove Ridge — Salinas de Chengue.

The gravel ridge separating the open and the closed lagoon (Fig. 30: 1-2) is settled on by the red mangrove *Rhizophora* mangle and has become stabilized by it. During dry seasons, the up to 1.5 m deep water in the shallow lagoon warms up considerably and evaporation is high. The lagoonal water therefore becomes more salinal than the sea water. During low tide, some of this water leaves the lagoon through a narrow channel. It is much heavier than normal sea water and does not readily mix with it. It flows into the open bay following the contours of the bottom and effecting the growth of corals. At high tide, normal sea water enters the lagoon through the inlet (Fig. 31). The bottom of the lagoon consists of soft mud, a few centimeters to up to 50 cm thick, on calcareous coral rubble. This calcareous mud contains a lot of organic matter. During rainy periods the lagoon may turn into brackish and even fresh water. Dead shells of *Assiminea* sp. and *Littoridina* sp. give evidence of such occurrences. During these times, the marine fauna in the lagoon is killed and fresh or brackish water run off through the narrow channel kills corals in the open lagoon of the bay.

Sea grass covers the Salinas de Chengue near the inlet. *Smaragdia viridis* is found here. Further inward only clumps of *Halimeda* are present with *Cerithium lutosum* (44), which is also found on the muddy bottom besides plants. *Crepidula convexa* (53) may be attached to their conchs. The high plankton production in the shallow warm water is used by numerous bivalves such as *Anomalocardia brasiliana* and a rich population of benthic worms. The clam is drilled by *Murex recurvirostris* (75), while the worms are preyed upon by *Conus jaspideus* (119), *Nassarius vibex* (104), and *Olivella perplexa* (115). *Melongena melongena* is only common near the inlet to the lagoon. At certain periods of the year, mass populations of *Finella dubia* (46), *Bulla striata* and *Tridachia crispata* occur, which are absent at other times of the year.

On the red mangrove *Littorina angulifera* (30) is found on the living wood up to where the first leaves lie. Dead branches and drift wood entangled between the roots of the mangrove are settled on by *Cenchritis muricatus* (32). This periwinkle, in contrast to its usual occurrence high up on cliffs, lives unusually close to sea level, but remains inactive for most times of the year. Only exceptionally rough conditions produce waves that spray this zone. Roots of the mangrove as well as gravel just above the intertidal zone show a mixed population of *Nodilittorina ziczac* (26) and *N. interrupta* (31). The prop roots of *Rhizophora* form a substrate for the oyster *Crassostrea rhizophorae* (= *virginica*) which is used as food by numerous large *Murex brevifrons* (77). *Littorina meleagris* (28) feeds on algal tufts covering all substrates in this area within the intertidal zone and just below it.

The high salinity water in the lagoon is quite turbid and unloads its organic suspension on its way out into the bay following the bottom of the open lagoon. These nutrients support a rich benthic fauna that is preyed upon by *Olivella petiolita, O. perplexa, O. adelae, Engoniophos unicinctus, Murex recurvirostris, Conus jaspideus, Terebra dislocata, Tornatina candei* and *Atys riiseanus*. The flora settling from it is collected by *Strombus pugilis, S. gigas* and *Bulla solida/striata*.

The hydroids *Halocordyle disticha* (c), *Myrionema hargitti* (a), *Garveia* sp., *Thyroscyphus ramosus* and *Plumularia halecoides* (b) are found on mangrove roots in the lagoon. They all tolerate turbid water. On the other side of the beach wall,

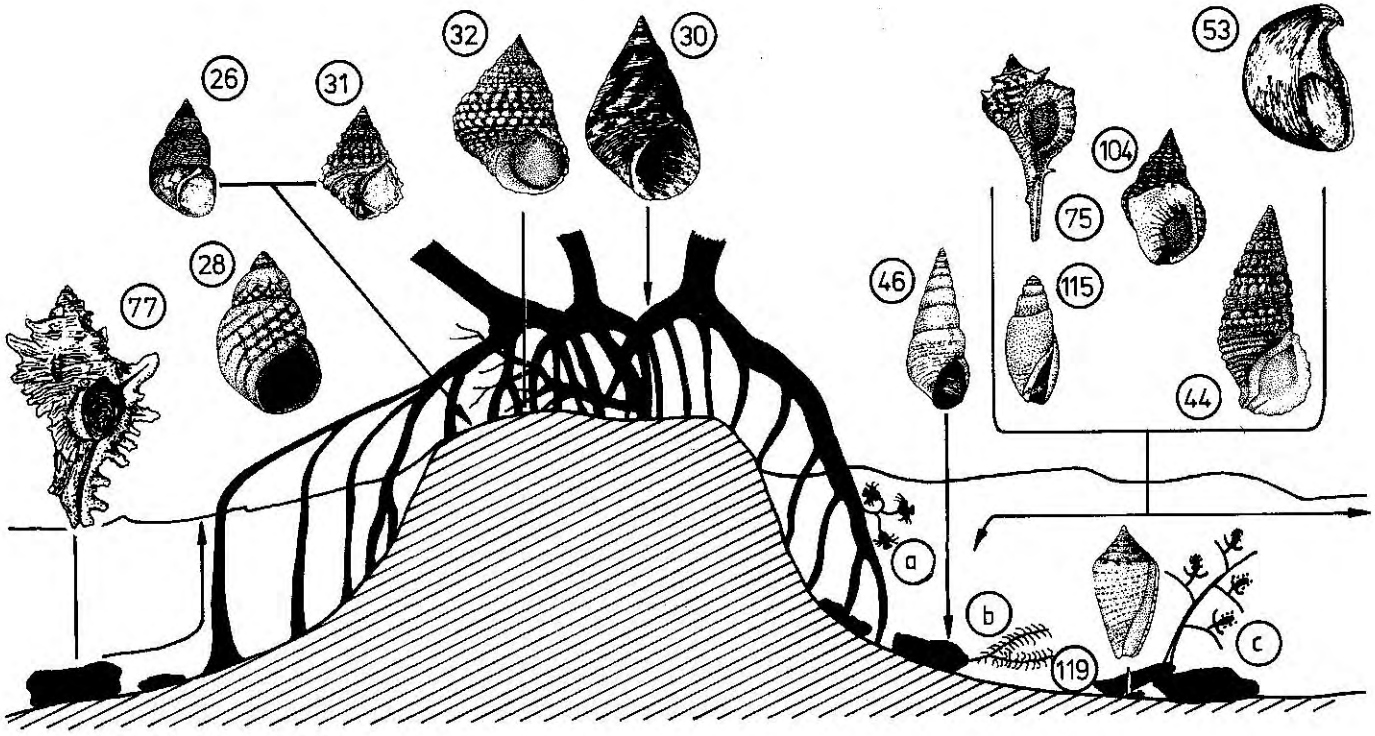


Fig. 31. A gravel ridge covered by mangrove trees separates the open lagoon from the closed lagoon in Chengue bay.

Abb. 31. Die offene Rifflagune wird von der Mangrove-Lagune in der Bucht von Chengue durch eine mit Mangrovebüschen bestandene Korallenschuttbarre getrennt.

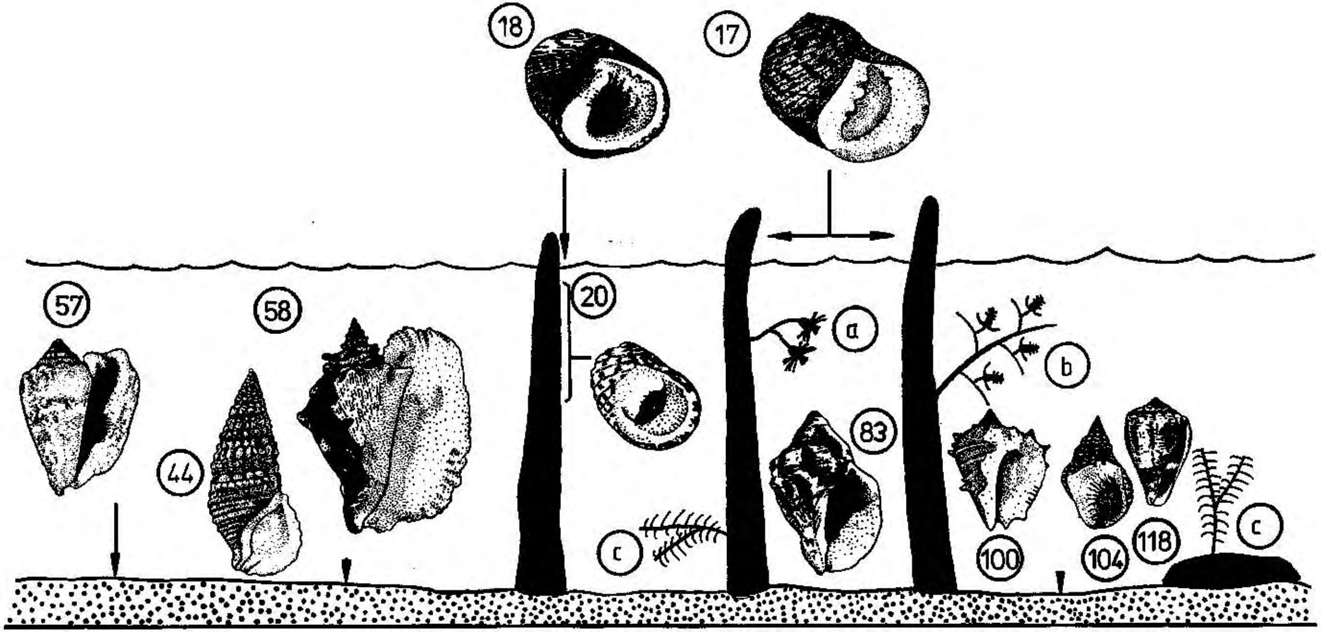


Fig. 32. Prop roots of the red mangrove at the shore of the Ensenada de Chengue provide substrate and environment for a number of molluscs and hydroids.

Abb. 32. Luftwurzeln der roten Mangrove im Strandbereich der Rifflagune der Bucht von Chengue sind von Mollusken besiedelt.

Halocordyle disticha, Eudendrium carneum, Thyroscyphus ramosus are present on the same substrate.

Prop Roots of the Red Mangrove.

The shore east of the bay head ends with a belt of mangrove forrest with muddy bottom and tree leaves, littering the floor with puddles of stagnant water (Fig. 30: 8). Here *Melampus coffeus* and *Neritina clenchi* live on the rotting leaves. On the opposite western side of the Chengue mangrove bushes have pushed their prop roots from sand, gravel and pebble bottom of the reef lagoon below low water line and have grown from here to above water surface to a hight exceeding high water line (Fig. 32). Juveniles of *Strombus gigas* (58) and *Strombus raninus* (57), *Cerithium lutosum* (44) feed on algae between the roots. *Melongena melongena* (100) searches the bottom for thin shelled gaping bivalves. *Conus mus* (118) and *Nassarius vibex* (104) look for worms. The roots provide the substrate for many organisms like the hydroids *Halocordyle disticha* (b), *Eudendrium corneum* (a), *Halecium halecium* (d), *Thyroscyphus ramosus* (c), *Plumularia helecoides* (e), oysters, balanids, tunicates, bryozoans and several species of algae. *Thais rustica* (83) feeds on balanids, while the other gastropods present here graze on algae. The zone just below water level at any tide shows *Nerita tessellata* (20). *N. fulgurans* (18) climbs up and down periodically leaving the water, while *N. versicolor* (17) stays above water surface on those portions of the prop roots which are rarely wettened by the sea.

Littorina angulifera may also be present here, but it prefers the branches of the mangrove to the roots.

Reef and Reef-Lagoon.

The western bay at the head of the Ensenada de Chengue is divided into a salina separated from the normal marine water by a continuous beach bar, a backreef lagoon, a well zoned coral reef and a seaward drop into the central bay (Fig. 30). The salina is inundated only during the wet season, whereas at dry seasons it forms a salt flat with continuously thickening stone salt due to sea water that seeps through the sand of the beach bar. This water evaporates within the salina. No molluscan and hydroid life is found in this lagoon, a few crabs are all that enter its seaward margin.

The reef lagoon and the reef are rich with fauna and gastropods living here are characterized in a numer of scetches in each of which only species of close systematic relation are considered.

The limpet-like archaeogastropods are represented with *Diodora listeri* (3) that lives on the underside of coral slabs in the lagoon as well as between corals and in the rubble on both sides of the reef (Fig. 33: A). *Fissurella angusta* (4) is common on the reef crest well camouflaged by calcareous algae and *Millepora; Hemitoma octoradiata* (6) is found on the whole reef crest, while *Fissurella nodosa* (5) browses only on the surf-swept portions. *Collisella antillarum* and *Acmaea pustulata* (7) are present on the surface of the reef crest as well as below rocks in this general area. A small variety of *Acmaea* settle on the leaves of the turtle grass off-reef. *Lucapina suffusa* prefers the underside of rocks, especially larger ones, found on both sides of the reef, where also *Diodora cayenensis* is found.

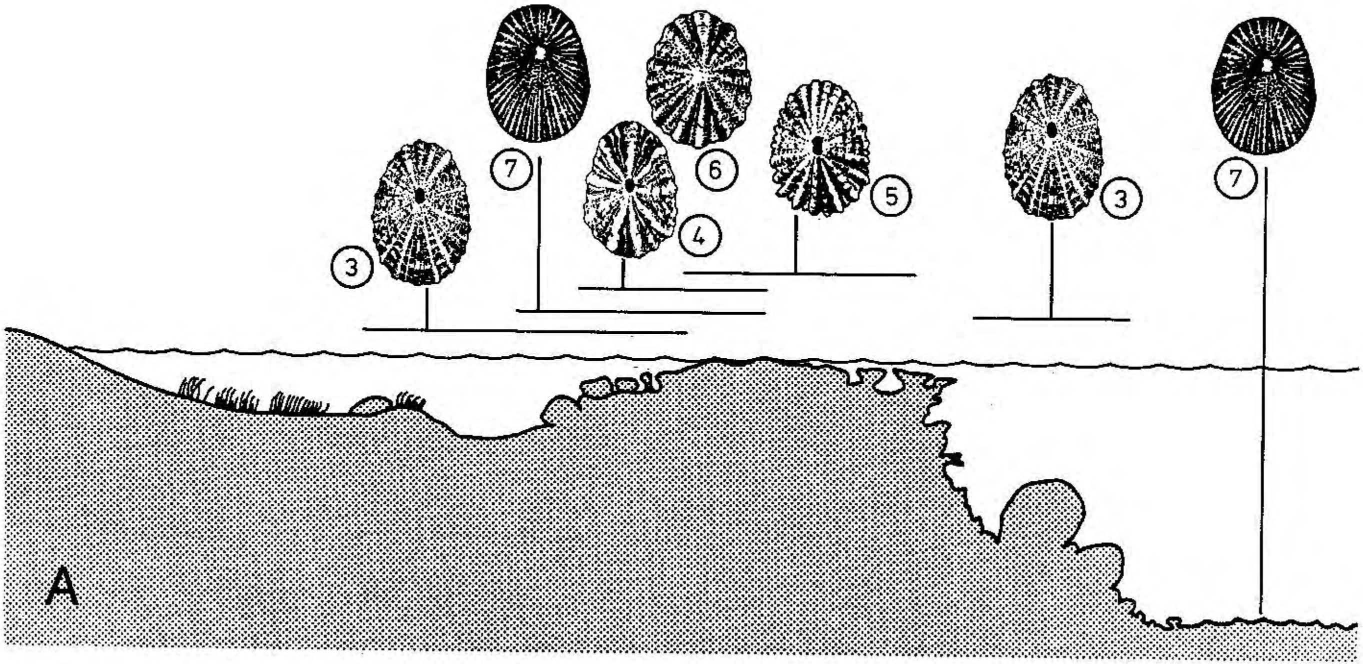
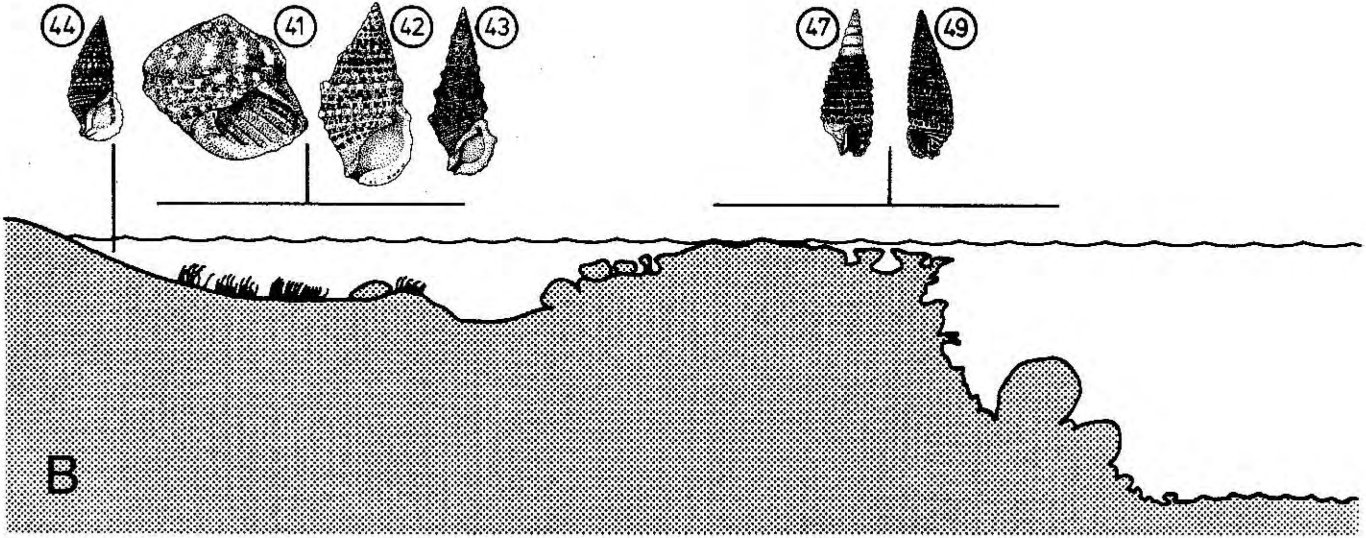


Fig. 33. Transect of the coral reef in the head of the Ensenada de Chengue from the lagoon to the open bay. — A. Archaeogastropod-limpet zonation. B. Cerithiacean-mesogastropod zonation. C. Tonnacean-mesogastropod zonation. D. Remaining mesogastropod and archaeogastropod zonation. E. Muricid-neogastropod zonation. F. Remaining neogastropod zonation.

Abb. 33. Querschnitt durch das Riff in der Bucht von Chengue von der Rifflagune bis zum offenen Buchtwasser. — A. Verteilung der napfförmigen Archaogastropoden. B. Verteilung der Cerithien-verwandten Mesogastropoden. C. Verteilung der Tonnaceen (höhere Mesogastropoden). D. Verteilung weiterer Archaeo- und Mesogastropoden. E. Verteilung der muriziden Neogastropoden. F. Verteilung aller übrigen Neogastropoden.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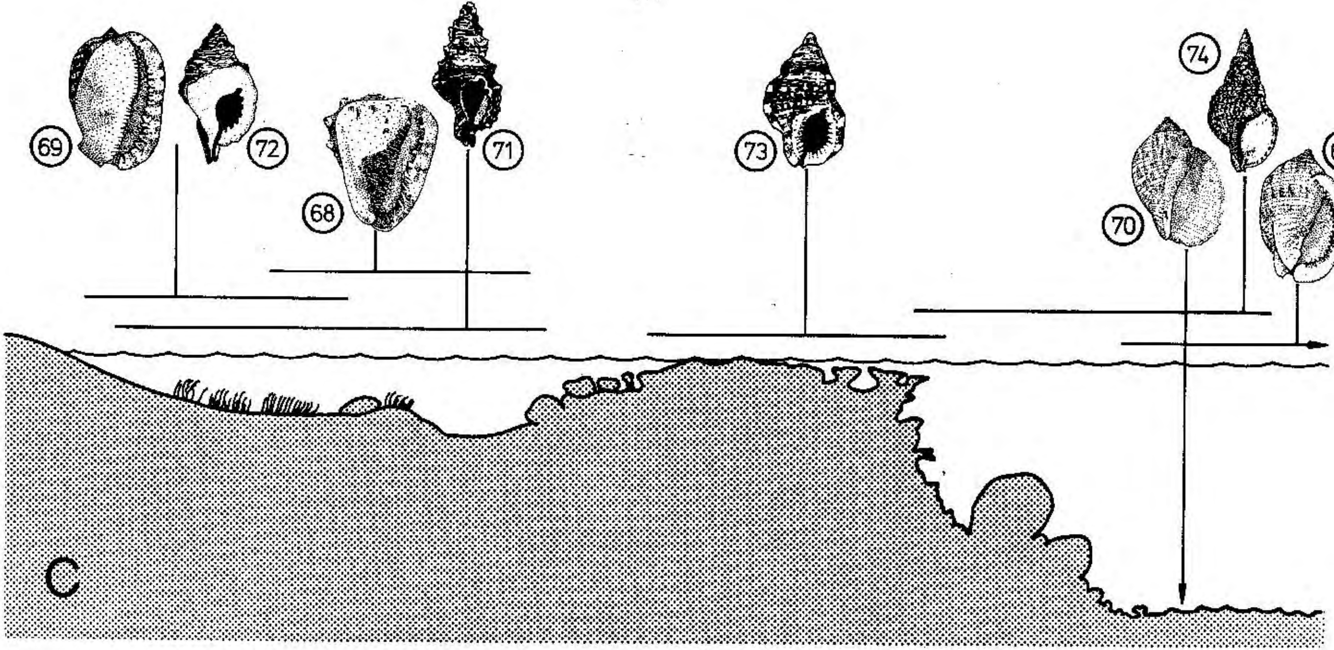
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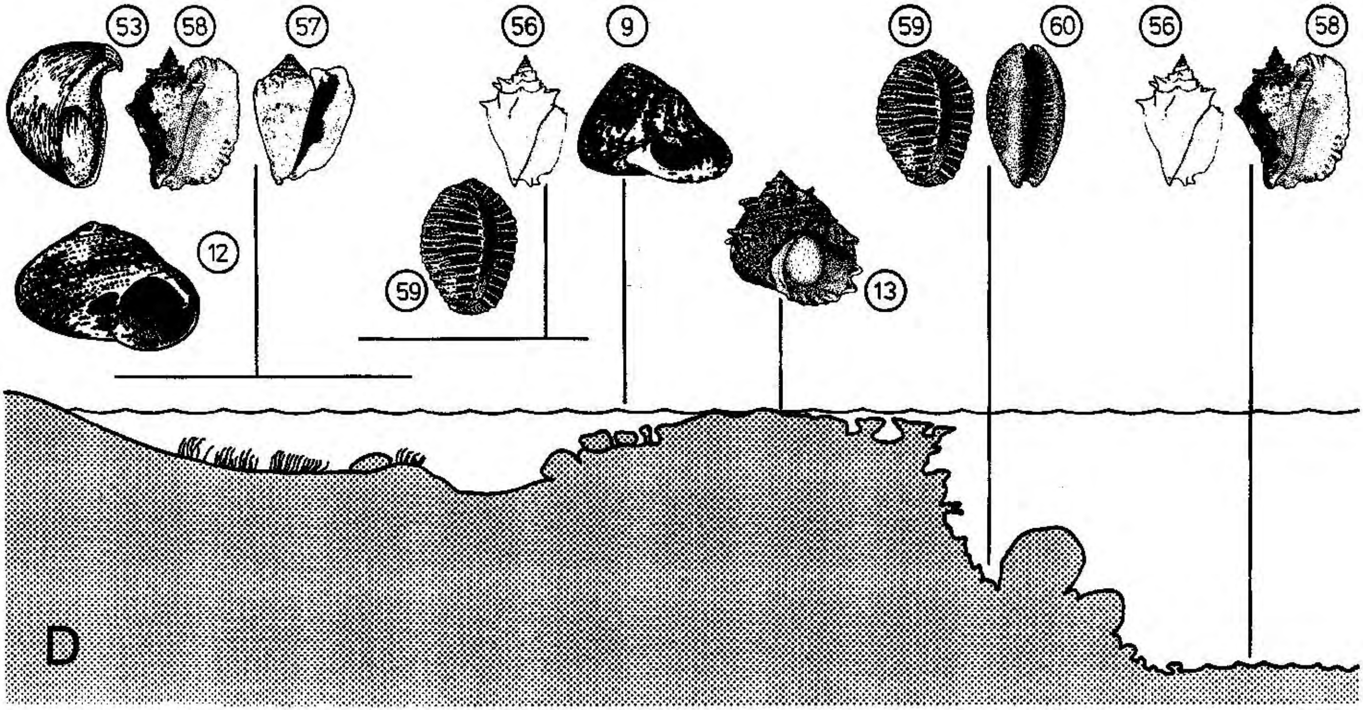
Cerithiacean mesogastropods begin their zonation with *Cerithium lutosum* (44) on sea grass in the intertidal zone of the lagoon (Fig. 33: B). The sea grass and the general sea floor of the subtidal lagoon supports large populations of *Modulus modulus* (41). *Cerithium atratum* (43) and *Cerithium litteratum* (42). Both species of *Cerithium* also occur in small numbers in pits and rubble fields of the reef crest. Characteristic cerithiids of the reef belong to the cerithiopsids (47) and triphorids (49) such as *Triphora turristhomae, Seila adamsi* and *Cerithiopsis emersoni.*

The tonnacean of most restricted portions of the lagoon (Fig. 33: C) is *Cymatium muricinum* (72) which tolerates both warm and saline water. The whole lagoon supports the common *Cymatium nicobaricum* (71), *C. pileare* and the rare *C. vespaceum, C. parthenopeum, C. krebsii. Cassis madagascariensis* (68) and *C. tuberosa* are found in the deeper lagoon up to the edge of the reef. Below reef debris on both sides of the reef crest, *Bursa granularis cubaniana* (73) is common. *Bursa thomae* is uncommonly found in crevices of the reef crest. *Cypraecassis testiculus* (69) hunts for irregular sea urchins in the sands of the lagoon, while the similar *Phalium granulatum* (67) searches for similar prey in the off-reef sands, where *Tonna galea* (70) hunts holothurians. *Charonia variegata* (74) preys on sea urchins such as the common *Lytechinus variegatus* in deeper water, but may also climb into the reef and enter shallow portions of the lagoon.

If we consider other mesogastropods and trochospiral archaeogastropods we can note that the strombids (Fig. 33: D) are distributed in such a way that *Strombus raninus* (57) lives in the shallow lagoon, *S. pugilis* (56) in deeper sea grass flats, young *S. gigas* (58) in shallow lagoons, old individuals of this species in deeper lagoons, here accompanied by *S. costatus,* and, very rarely, by *S. samba. Trivia pediculus* (59) can be found under rocks in the shallow lagoon as well as in the deeper one and on the sides of the reef, while *Cypraea cinerea* and *C. cebra* (60) prefer the rocks on the flanks of the reef. *Zebina browniana* and other rissoids are found in algal growths and *Crepidula convexa* (53) is attached to several lagoonal gastropods, especially *Tegula fasciata* (12), which is common on coral slabs in the shallow lagoon. *Turbo castanea* is also found here, whereas *Tegula viridula* (9), *Arene tricarinata* and *A. cruentata* settle the edges of the reef. *Astraea caelata* (13), *A. tuber* and *A. tecta* roam the reef platform.

Muricid neogastropods (Fig. 33: E) have their most shoreward representative in *Thais rustica* (83) which occurs regularly on large logs and mangrove roots in the intertidal zone. *Murex recurvirostris* (75) rests in soft lagoonal sediments, preferably in the shallow lagoon, while *M. pomum* (76) prefers deeper lagoons. *Murex brevifrons* (77) is found on hard substrates in all water depths. *Thais deltoidea* (82) lives on the wave-swept reef crest and has an algal and milleporan encrusted shell, as *Morula nodulosa* (78) also does. *M. nodulosa* prefers the more exposed seaward side of the reef crest. *Aspella anceps, A. paupercula* and *Favartia cellulosa* are found below dead coral near the reef crest. *Coralliophila abbreviata* (86) feeds on living stone corals of the entire reef, while *C. caribbaea* (85) is found on *Gorgonia* of the seaward reef slope. *Ocenebra rosea* (79) lives on the lower side of coral slabs, especially on the seaward reef slope. The sandy bottom at the base of the reef is settled on by *Ocenebra* sp. (127).

Of the buccinacean neogastropods (Fig. 33: F) *Engoniophos unicinctus* (99) and *Nassarius vibex* (104) live in the mud and sand of calm intertidal regimes of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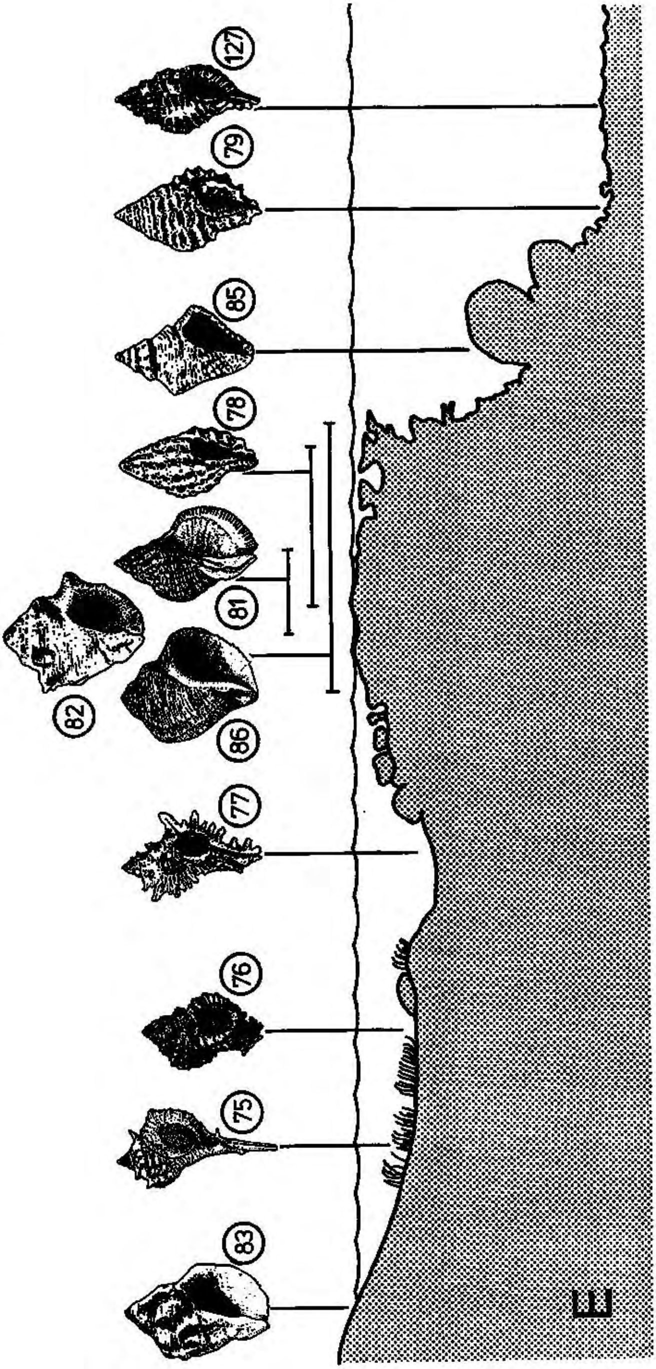
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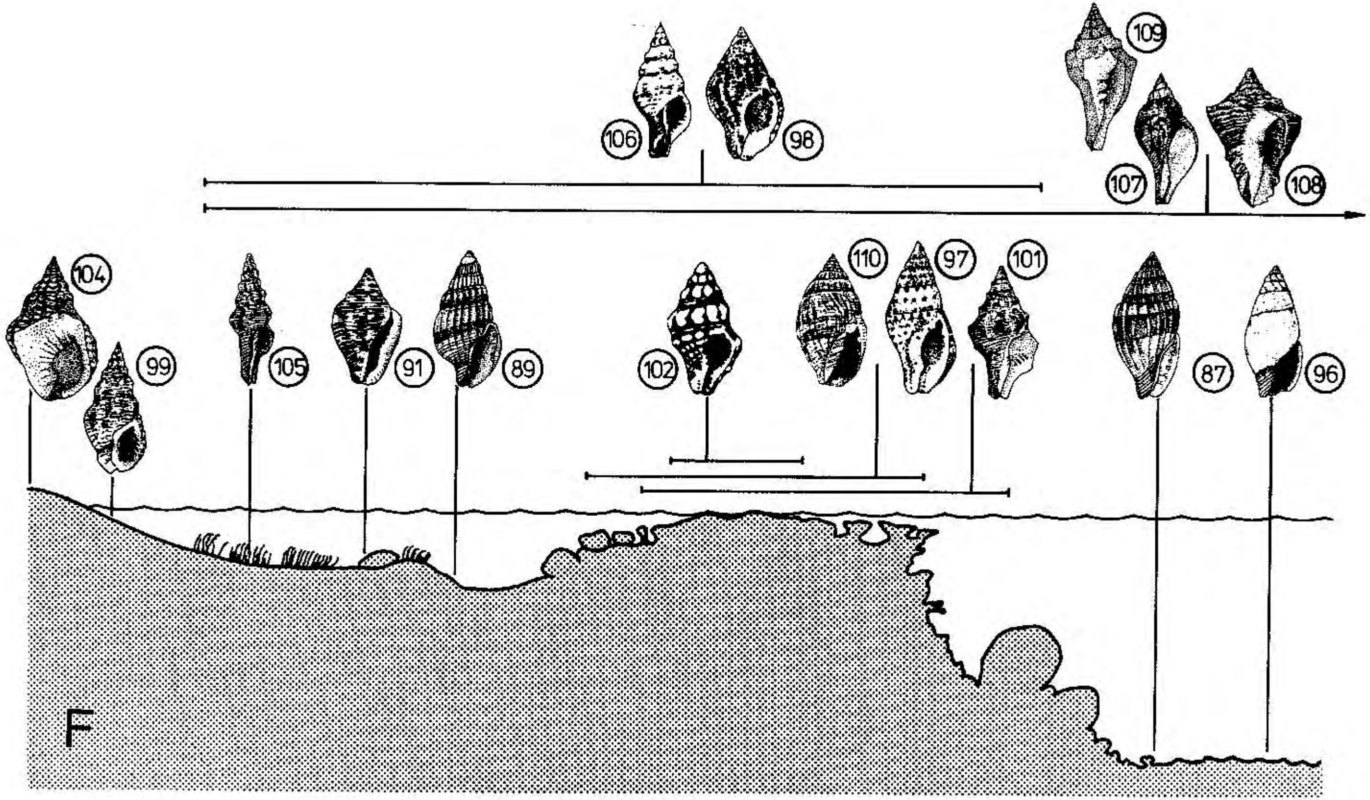
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the lagoon. Coral fragments scattered throughout the lagoon can have *Latirus infundibulum* (105), *Anachis pulchella* (89) and *Engina turbinella* on their undersides and *Columbella mercatoria* (91) on their upper surface. *Mitra nodulosa* is found here too, but rarely. *Turbinella angulata* (109) and *Fasciolari tulipa* (107) enter the lagoon and also the reef rubble. *Vasum muricatum* (108) prefers reef rubble on both sides of the reef crest. All of the three last named large gastropods are more common in the off-reef sands. The whole reef platform is settled on by *Pisania pusio* (97) and *Leucozonia nassa* (101), while *L. ocellata* (102) and *Vexillum puella* (110) prefer only the wave-swept upper platform. Reef rubble on both sides of the reef is settled on by *Latirus angulatus* (106) and *Pisania auritula* (98), along with *Anachia pulchella*. *Anachis obesa* (87) and *Mitrella lunata* (96) are found on off-reef sea grass. *Morum oniscus* lives among lagoonal coral debris.

Of the cones, *Conus mus* is to be found everywhere in the lagoon, and also in the reef together with *C. regius*, *C. ermineus* and *C. insularis*. In the off-reef sands, *Conus jaspideus* is common, along with different species of *Terebra* and turrids. Only the turrids *Crassispira albumaculata* and *Drillia solida* live in the algal milleporan ridge of the reef.

A similar occurrence of gastropod species can be observed in the reefs and lagoons of the other bays of Cinto, Gayraca, Nenguange and Arrecifes.

The hydroid fauna of the coral reef is very poor. In well-illuminated moderately exposed spots live small groups of *Halocordyle disticha*. These form larger colonies as those found on the rocky shore, but are much less abundant on the reef. On dead coral in shallow parts of the reef few colonies of *Dynamena cornicina*, *Halopteris diaphana* and *Lytocarpus philippinus* are found.

Sea-Grass and Coral Slabs in the Reef Lagoon.

The turtle-grass and limestone slabs form substrate for characteristic animal communities with quite a number of gastropods and several hydroids that show some differences in species composition to the same substrates in open bays (Fig. 34). *Modulus modulus* (41), *Cerithium atratum* (43) and *Cerithium litteratum* (42) feed on algal covers on the grass as well as on the bottom between plants. *Smaragdia viridis* (22), *Phyllaplysia engeli*, *Phenacolepas hamillei* (23) are present on the leaves and, in addition characteristic small shells of a species of *Acmaea* (7). *Anachis obesa* (87) searches for hydroids such as *Dynamena cornicina* (c), *Sertularia inflata* (b) and *Plumularia strictocarpa* (a). Leaves and, more often, roots are covered by *Millepora squarrosa*.

Limestone slabs broken from the coral growths and reefs during heavy storms are scattered throughout the lagoon and provide a living and resting place for many species of gastropods and chitons. *Ischnochiton pectinatus*, *I. papillosus*, *Stenoplax limaciformis*, *Acanthochitonia hemphilli*, *Collisella antillarum* (7), *Diodora listeri* (3) and *Hipponix antiquatus* (50) are present. Algae are grazed on and collected by the common *Tegula fasciata* (12) the more rare *Arene tricarinata* and the small snails *Caecum nitidum* (35), *C. pulchellum* (34), *Diastoma varium* (45) and *Finella dubia* (46). The lower side of the rocks accomodates gastropods of nocturnal activity such as *Bursa granularis cubaniana* (73), *Cymatium pileare*, *Morum oniscus*, *Pisania pusio* (97), *P. auritula* (98), *Anachis pulchella* (89), *Dendrodoris krebsii*, while other predators usually remain in this environment, i. e. *Cypraea cinerea, Trivia pediculus* (59), *Aspella paupercula, Engina turbinella, Columbella mercatoria* (91). *Hyalina avena* (116) and *Mitra nodulosa* are found on and below the slabs. Large gastropods visit these hard substrates sporadically to feed on bivalves such as *Murex brevifrons*

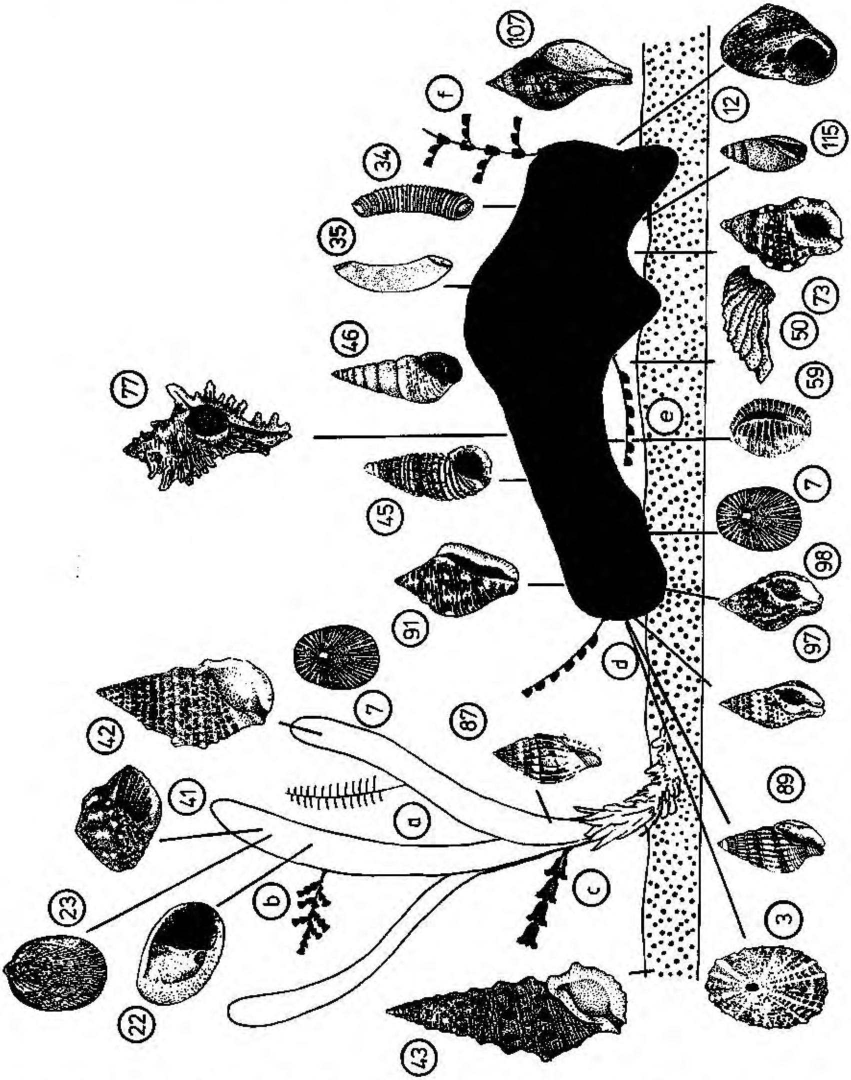


Fig. 34. Sea grass and slabs of dead corals in the reef lagoon provide living space for many molluscs and few hydroids.

Abb. 34. Seegras und tote Korallenblöcke sind im Bereich der Rifflagune von Mollusken dicht besiedelt.

(77), to hunt gastropods such as *Fasciolaria tulipa* (107), and to graze algae such as *Turbo castanea*. The hollow base of the slabs is settled on by the hydroids *Antenella* sp. (e), another species of which is also found on the outer slab surface (d), together with *Halopteris diaphana* (f).

Hollow Brain Coral.

Hemispherical coral colonies similar to those produced by *Diploria* are found on the lagoonal slope of the reef and have often been bioeroded from below by boring organisms. They represent a typical environment (Fig. 35).

Coralliophila abbreviata (86) lives on the outer surface of the coral colony and feeds on the tissue of the polypars. Most gastropods, however, prefer the shelter of the hollow base of the colony. Here walls are covered by crust-forming sponges, tunicates, corals, bryozonas. Hydroids such as *Zanclea* sp., *Turritopsis nutricula*, *Clytia striata*, *Dynamena corticina* and *Antennella nutricula* are present. *Diodora listeri* (3), *Lucapina suffusa* as well as different species of *Triphora* (49) and *Cerithiopsis* (47) feed on sponges while *Trivia pediculus* (59) *Cypraea cebra* (60), *C. cinerea* and rare *C. spurca acicularis* mainly feed on tunicates. *Conus regius* (120) and *C. ermineus* are usually hidden in the sand below the cavity and utilize the walls to attach their egg cases. The chitons and gastropods *Latirus angulatus* (106), *Ocenebra rosea* (79), *Mitra nodulosa*, *Pusia auritula* (98), *Ischnochiton pectinatus* and *Stenoplax limaciformis* are present.

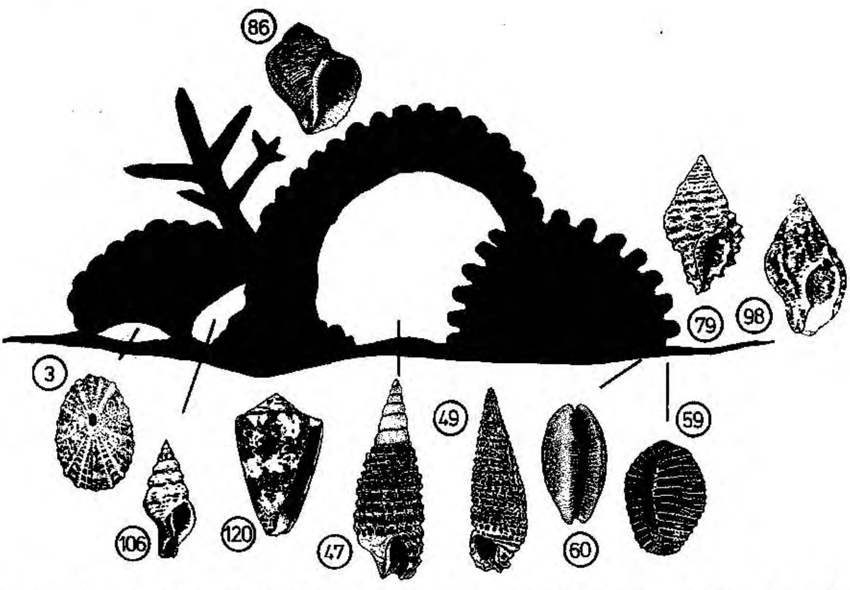


Fig. 35. Growing brain corals in the lagoonal reef have usually been excavated from below by boring organisms and provide good shelter for numerous organisms.

Abb. 35. Im Schutz des Riffwalles wachsende Hirnkorallenknollen sind oft von unten her angebohrt und ausgehöhlt. In diesem Bereich finden zahlreiche Tierarten Schutz.

Seaward Reef Slope.

The dominating organisms on the seaward slope of the coral reef of Chengue (Fig. 36) are *Acropora palmata* and *Millepora squarrosa*, but other stone corals such as *Agaricia*, *Porites* and *Diploria* and the soft coral *Palythoa* are also present. *Gorgonia*-sea fans are attached to corals and support *Simnia acicularis* (61), *Cyphoma gibbosum* (62) and *Coralliophila caribbaea* (85) which live on its tissue. The hydroids *Halocordyle disticha, Halecium halecinum, Eudendrium carneum, Dynamena cornicina* and *Lytocarpus philippinus* are characteristic of this zone in the reef. Crustal sponges are settled by several species of *Triphora* (49) and of *Cerithiopsis* (47). The tunicates are scraped by *Cypraea cebra* (60) and small bivalves are drilled by *Ocenebra rosea* (79). Living corals provide food for *Coralliophila*

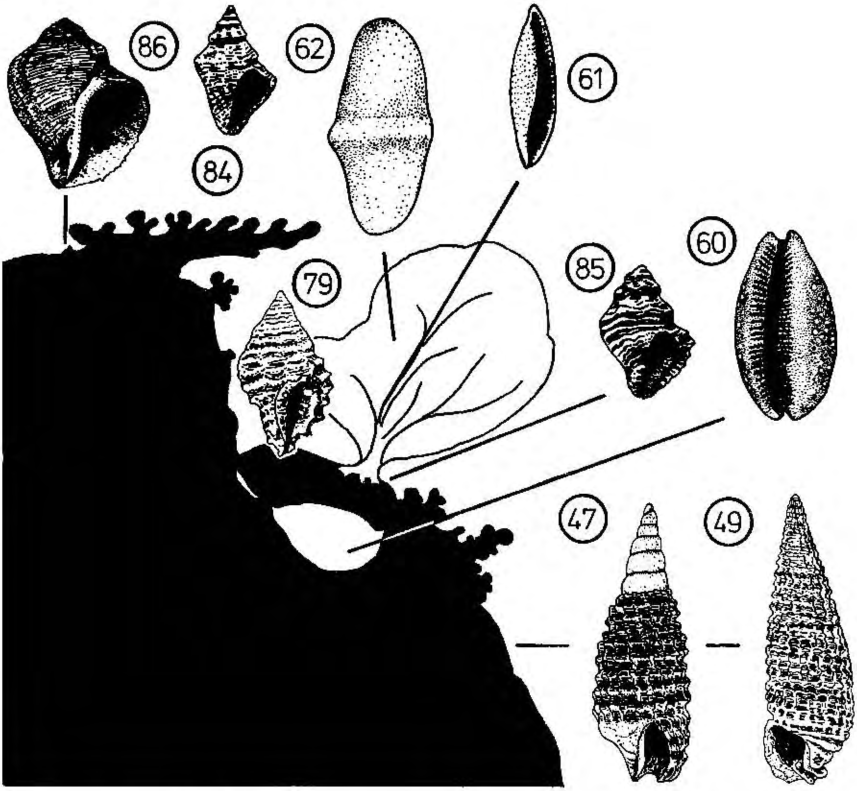


Fig. 36. The seaward reef slope is dominated by numerous growing corals, other coelenterates and sponges. Gastropods here live on these.

Abb. 36. Die seewärtige Seite des Korallenriffes ist dicht von lebenden Korallen, anderen Coelenteraten und Schwämmen bedeckt. Gastropoden leben hier zumeist von diesen Organismen.

abbreviata (86) and *C. aberrans* (84). This association is found wherever corals and gorgonians grow on a slope and it is present on the off-reef slope as well as on cliffs or beach rock bars as that in Arrecifes bay.

Cienaga Grande Lagoon.

The Cienaga Grande de Santa Marta is the largest lagoon on the Caribbean coast of Columbia. The lagoon lies within the delta of the Rio Magdalena and is situated between the mouth of the river and the Sierra Nevada de Santa Marta. The lagoonal shore consists of mangrove swamp composed of *Rhizophora mangle* at the shores and *Avicennia nitida* within the forrests. Only part of the sandy coastal bar separating the lagoon from the open sea (Isla Salamanca) has been cleared of mangrove forrest by humans (Fig. 37).

Several rivers flow into the Cienaga Grande, deriving their water from the Sierra Nevada. Rio Fundacion, Rio Sevilla and Rio Frio are the three largest of these. The mangrove swamp is continuous up to the shores of the Rio Magdalena. At high floods of the river, fresh water moves overland through the mangroves and through a man-made canal (Caño Clarin). The Cienaga Grande, in its NE-corner opens into the sea.

The lagoon is shallow with an avarage depth of 1-1.5 m and, rarely, 3 m. The bottom is covered with a mixture of soft clay and organic mud. Within the channel leading to the sea (Boca) and the estuarine zone shill and sand beds are present as well as oyster banks.

Salinity within the lagoon is not stable. Two parts of the lagoon can be differentiated: the first is closely connected to the sea and is characterized by changes of salinity during most of the year; the second is the larger one (15 × 30 km) and its salinity is only affected by seasonal changes. The salinity of the main body of the lagoon is determined by three factors; 1.) evaporation; 2.) tidal exchange of sea water; 3.) fresh water discharge of the rivers. During the dry seasons of the year the discharge of fresh water decreases, and the suction caused by evaporation increases. As a result sea water enters the lagoon and the salinity of its water is raised. Extreme and exceptional salinity measured in the main body of the lagoonal water may reach 40‰. Normally, the highest salinities reached within a year's time are around 20‰ and near river mouths, 10-15‰. At the end of the rainy season, fresh water runoff from the interior of Columbia reaches the area of the Rio Magdalena delta and results in a flood that pushes fresh water through the mangrove swamps and the canal. The whole lagoonal water may be pushed out into the sea and be replaced by fresh water. During such floods, usually of short duration, the Boca of the lagoon turns into the mouth of a fresh water river; and additional openings may form and channels may be eroded into the sand of the Isla de Salamanca. Every 6-10 years the flood is very high and lasts for several months, during which the lagoon becomes a fresh water lake. Between extremes of high salinity, following weak rainly seasons and the fresh water of the floods, the Cienaga Grande is filled with brackish water of about 10-25‰ and has temperature of 26 to 32 C° for most of the year.

Three types of organisms live in the lagoon as a result of the changing salinities. The first type is made up of animals that tolerate all conditions and remain alive during the different periods of the year, such as the hydroid *Calyptospadix cerula*

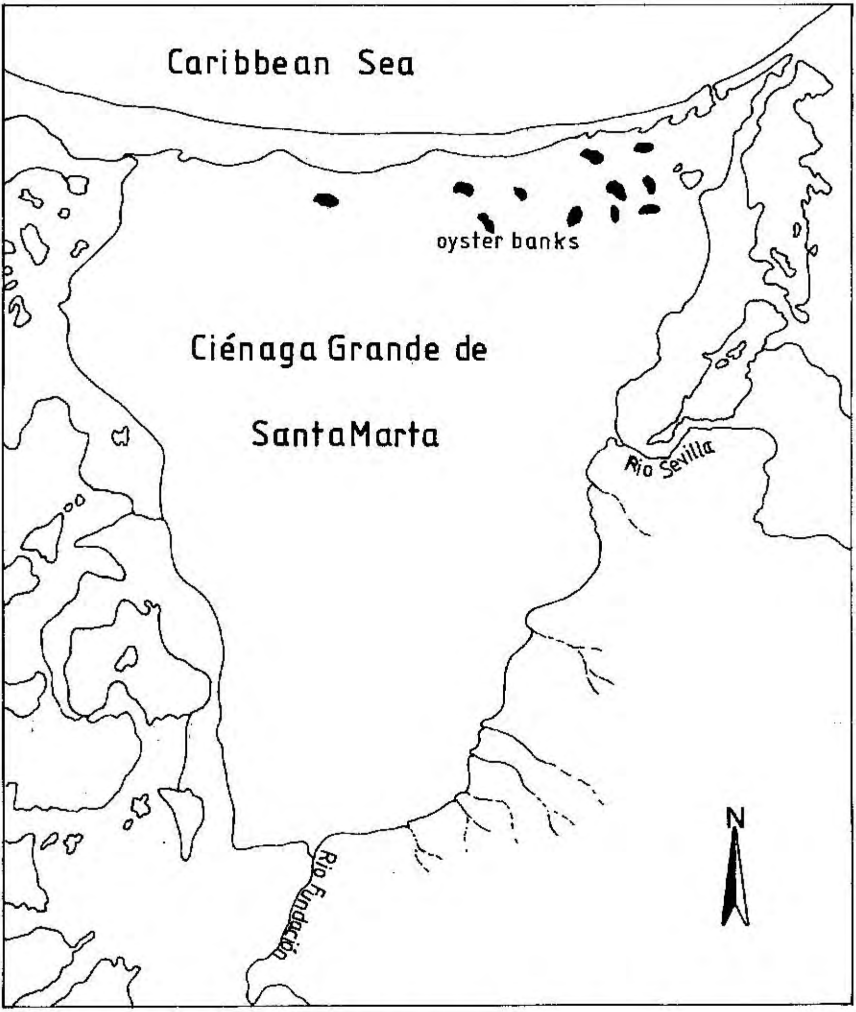
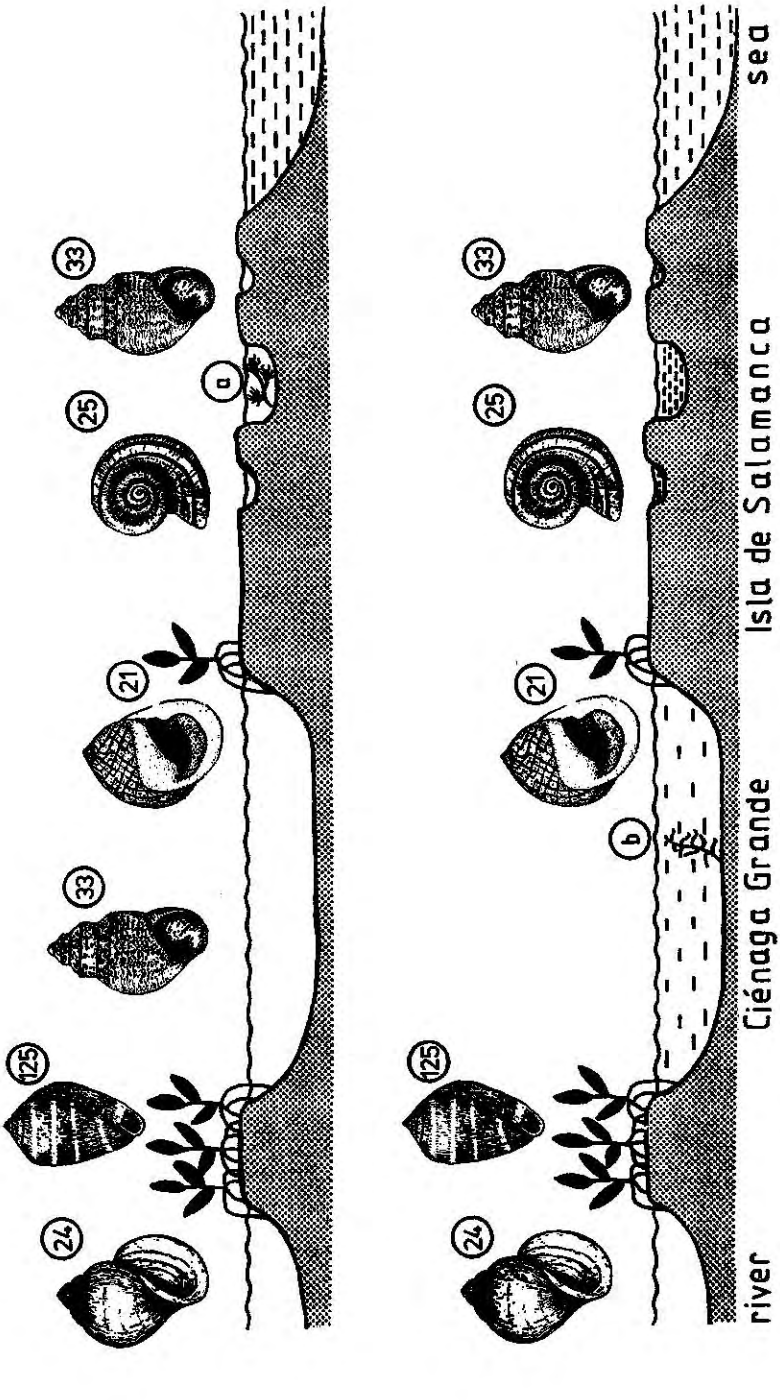


Fig. 37. Map of the large lagoon of Cienaga Grande. This body of shallow water is usually brackish.

Abb. 37. Karte der Brackwasserlagune Cienaga Grande.

(= *Garveia franciscana*), the bivalves *Polymesoda arctata* and *Crassostrea virginea* (= *rhizophorae*). The second type consists of periodical immigrants which come from the sea. Within this type, it is possible to differentiate two groups, the first of which have one part of their ontogeny restricted to the lagoon and the second, which come from the sea as periodical immigrants to exploit favourable conditions once salinity is high enough. Many shrimp, some marine fish-larvae and catfish belong to the first of these subgroups of the second type of organisms. Whereas the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fish usually live in the lagoon during their young life, the shrimp migrate into the lagoon from the sea, grow to large size here and then imigrate into the sea again later. The second of these subgroups are represented by hydroids such as *Clytia striata*, *Obelia dichotoma* and *Obelia bidentata* which settle on hard substrates and mature rapidly; by sponges that grow fast and serve as hosts for *Triphora nigrocincta;* by actinians such as *Aiptasia* which serve as food for *Epitonium lamellosum*, by balanids, lobster, sharks and bony fishes.

The third type of organisms come from a fresh water environment. As in the second type two groups can be differentiated; one with animals spending part of their life in the lagoon and then returning into the rivers, like the fresh water shrimp *Macrobrachium*. It develops its eggs and the first larval stages in the lagoon before it returns into the rivers. The others, such as the hydroid *Cordylophora caspia*, the gastropod *Assiminea succinea* and the bivalve *Mytilopsis sollei* are only present when the lagoon is a fresh water lake.

Periodic Changes in the Delta Lagoon — Cienaga Grande de Santa Marta.

The very generalized section is drawn to show fresh water (Fig. 38, left), mangrove forrest and the lagoon (Fig. 38, centre), mangrove and fresh water ponds of the beach bar and the open sea (Fig. 38, right). The upper scetch shows conditions during a flood, the lower one during dry seasons.

Fresh water in rivers is populated by *Ampullarius monticolus*, and *A. porphyrostomus* (24) and *Marisa cornuarietis* (25) occur in lakes. *Melampus coffeus* (125) and *Neritina clenchi* live in the mangrove forest on the muddy ground which is littered with leaves. *Neritina virginea* (21) settles on mangrove roots and more solid grounds within the estuarine areas. *Melampus* and *Neritina* live only in areas which, at least for a short period within a small number of days, is flooded by marine or near-marine water which takes freshly hatched veligers into the sea and brings larvae ready to settle from the sea. The larvae of *Melampus* and *Neritina* from the Cienaga Grande have to be able to reach the open sea where they swim actively for some weeks and feed on phytoplankton. *Melampus* and *Neritina* are, therefore, only found in parts of the lagoon close to the estuarine region.

The molluscan fauna of the Cienaga Grande is split into 4 groups:

1. fresh water species like *Ampullarius*, *Marisa* and *Assiminea;*
2. lagoonal species such as the bivalve *Polymesoda;*
3. species of the mangrove forrest near the estuarine zone like *Melampus* and *Neritina clenchi;*
4. gastropods and bivalves of the estuary such as *Neritina virginea* and *Crassostrea virginica*.

◀ Fig. 38. In the Cienaga Grande, drastic faunal changes are brought about by periodic floods of fresh water which flush out the salty water, but do not imprint themselves strongly on mollusc occurrence.

Abb. 38. Im Bereich der Cienaga Grande-Lagune bewirken periodisch wiederkehrende Fluten des Rio Magdalena einen sehr drastischen Faunenwechsel durch völliges Ersetzen des Brackwassers durch Süßwasser. Auf die Molluskenverteilung hat das aber keinen sehr starken Einfluß.

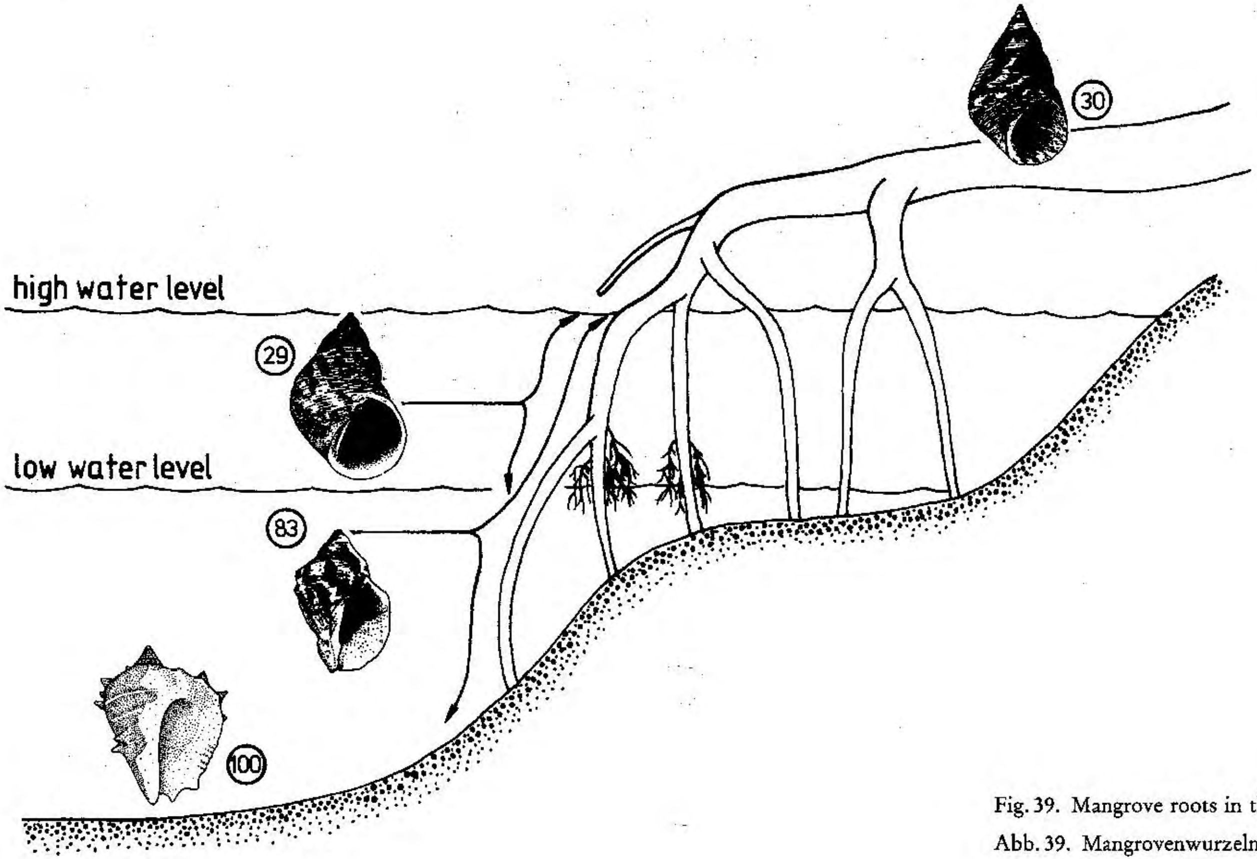

Fig. 39. Mangrove roots in the estuary.

Abb. 39. Mangrovenwurzeln im Ästuar.

The conspicuous white egg masses of *Ampullarius porphyrostomus* clearly mark the border between fresh and brackish water. When the lagoon is flooded by fresh water, *Ampullarius* and *Marisa* spread rapidly and throughout clinging to the drifting water hyacinth *Eichhornia crassipes*. However, populations will not increase much in numbers due to the fact that embryonic development is long (Bandel 1976) sometimes longer than the flood lasts. In *Assiminea succinea* embryonic development is more rapid, and 3-12 weeks are sufficient for mass populations to form on the muddy bottom as well as on the thalli of the fresh water alga *Elodea* that grows and spreads in the lagoon at an even faster rate than *Assiminea* does. The hydroid *Cordylophora caspia* (a) joins *Assiminea* on *Elodea* and is found throughout the year in fresh water pools. When the lagoon is brackish, *Cordylophora, Assiminea* and *Elodea* disappear. The hydroid *Calyptospadix cerula* (b) survives the fresh water period with the help of a resting phase and becomes active again when salinity rises. *Crassostrea virginica* survives fresh water floods by resting and keeping its valves closely shut. During this time, the oyster switches from aerobic to unaerobic metabolism and stays alive for up to 8 weeks without much harm and resumes normal activity in saline water. A longer period of fresh water kills oysters and none survived a flood of ten weeks.

Mangrove Roots in the Estuary.

In the estuarine zone of the mouth of the Cienaga Grande salinities change in dayly rhythm and tidal currents sweep oceanic water in and out. With exceptión of extreme periods of floods, the strongest influence comes from the open sea (Fig. 39). But only species showing extreme adaptability can enter this area of rapid changing conditions. Only two species of sponges, no octocorallians and madreporians, a few bryozoans, but no echinoderms and no tunicates are present.

The hydroid *Calyptospadix (Garveia) cerula* is attached to the roots of *Rhizophora mangle*. In the supratidal zone, *Littorina angulifera* (30) is present while *Littorina nebulosa* (29) grazes within the intertidal zone. *Thais rustica* (83) and *Thais trinitatensis* (Guppy 1869) feed on barnacles and the muddy bottom between roots supports *Melongena melongena* (100) in search of gaping bivalves *Tagelus plebeius*.

Rocky Shore in the Estuary.

Rocky constructions along the tidal channel and oyster reefs (Fig. 40) support populations of the hydroids *Calyptospadix (Garveia) cerula* (a), *Clytia striata* (b), *Obelia bidentata* and *O. dichotoma*. *Littorina nebulosa* (29) graze on the intertidal zone. Bivalves such as *Crassostrea virginea, Brachydontes exustus* and *Isognomon alatus* are attached to the rocks or to oyster-shells. These may be preyed on by *Thais haemastoma* (81), *Thais rustica* (83) and *T. trinitatensis*. At fresh water floods, *Mytilopsis sallei* can be found here. However it does not survive the return of changing salinities.

Mass mortality of benthic animals in the estuarine region is not only associated with salinity extremes, but also occurs after strong plankton blooms. The mass production of certain Cyanophyceans, for example, killed a rich *Polymesoda* population that had survived throughout all salinity changes without being harmed.

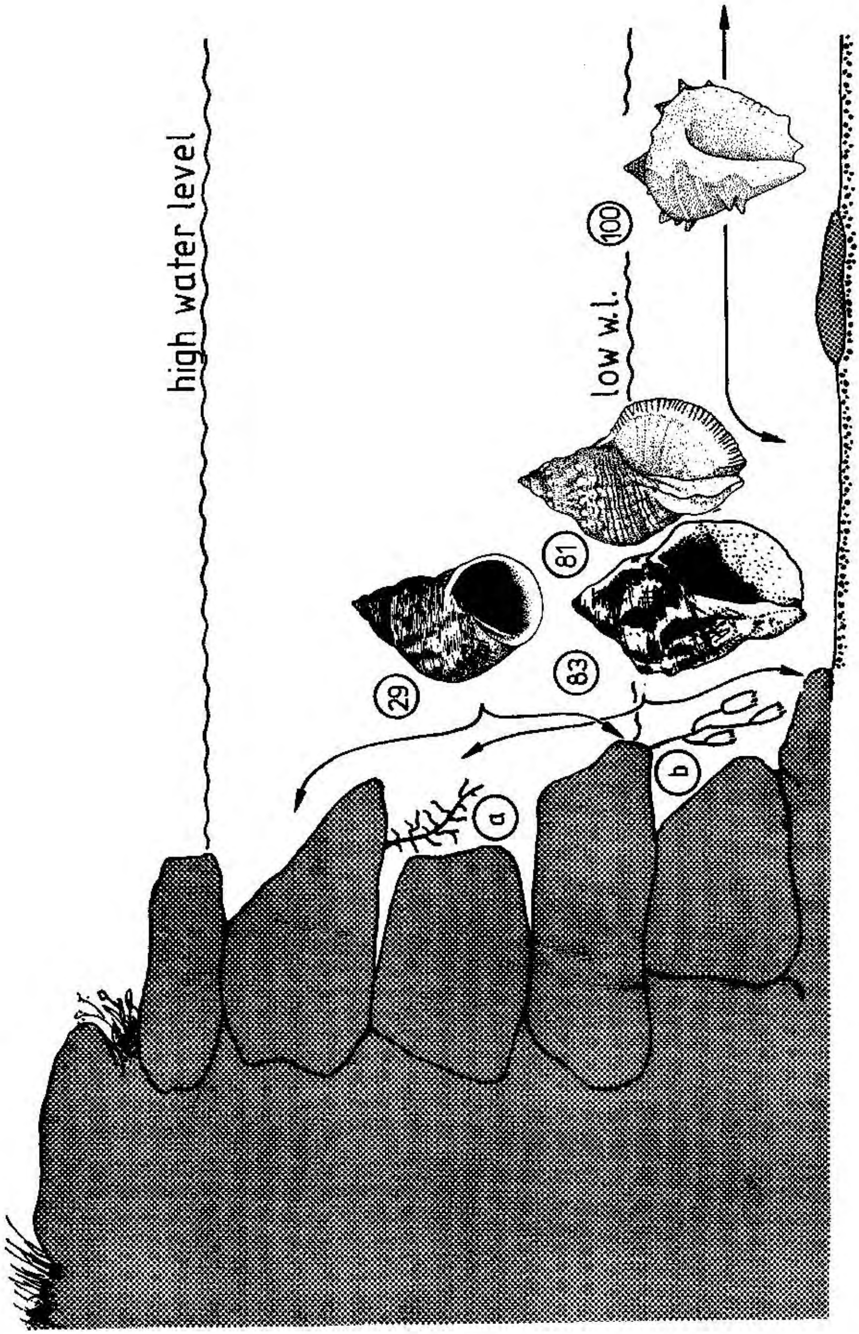

Fig. 40. Rocky shore in the estuary.

Abb. 40. Steinverbauungen im Ästuar.

Morphology in Relation to the Environment.

Gastropoda.

The approx. 250 species considered in this study vary considerably in size. The majority of adults is bigger than 5 mm and smaller than 50 mm. Only about 30 species are smaller than 5 mm and about the same number are larger than 50 mm. Members of the genera *Barleeia, Amphithalamus, Cingulopsis, Rissoella, Caecum* (35), *Marginella* and *Cylichnella* do not grow larger than 3 mm, and all live in algal thickets. They do not graze, rake or bite their food but collect minute particles and swallow them as whole. As regards their shape, they are different from each other and, in this respect, are like other small species.

Among species of not more than 5 mm in shell size, a variety of feeding types is developed. A few of these are shown in Fig. 41. *Collisella* (7) and *Arene*, for example, scrape up hard, calcareous algae, *Tricolia* (16) and *Littorina meleagris* (28) graze on soft algae, *Assiminea* (33), *Zebina, Diastoma, Finella* (46) and *Atys* collect plant and other small particles, *Anachis obesa* (87), *Mitrella lunata* (96), *Nassarina* and *Aesopus* feed on animals tearing tissue with bites of the radula situated in the end of the trunk-like proboscis, *Olivella perplexa* (115), *O. petiolita* (113) and *Marginella lavalleana* swallow animals whole. There is a large variety of shapes (Fig. 41): Limpets (7) (*Collisella* sp.) are present as well as short trochospiral forms

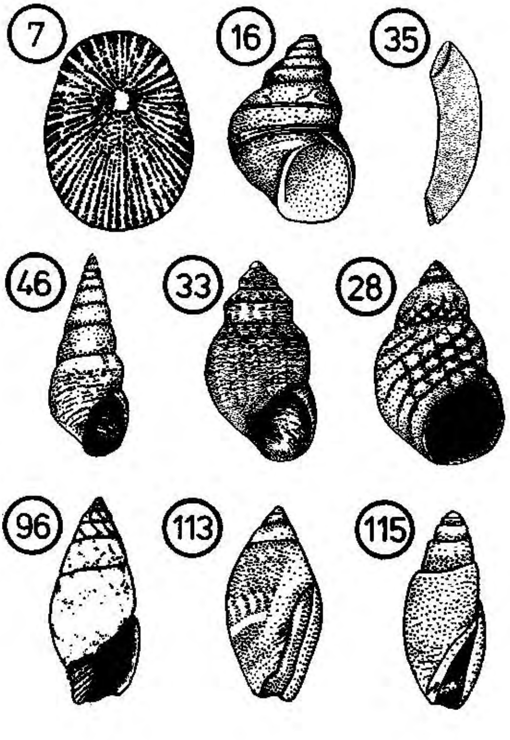

Fig. 41. Gastropods of different systematic origin that are united by their small size as adults, below 5 mm.

Abb. 41. Schnecken verschiedener systematischer Zugehörigkeit mit Adultgehäusen nicht größer als 5 mm.

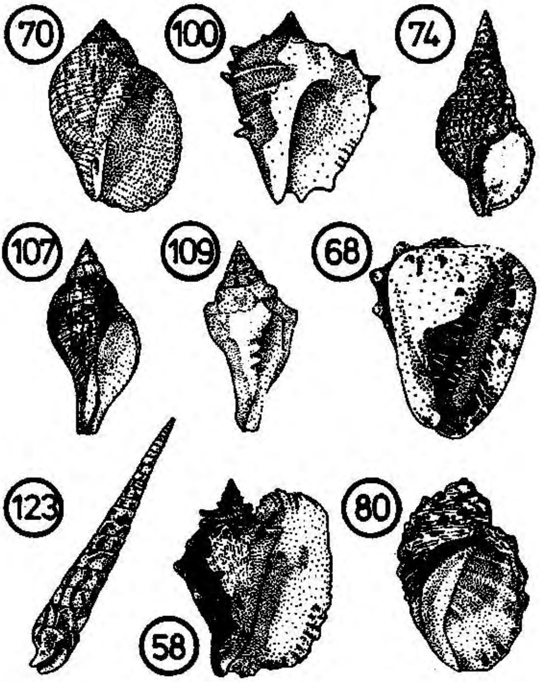

Fig. 42. Compilation of gastropods that are larger than 100 mm.

Abb. 42. Zusammenstellung von Schnecken, die größer sind als 100 mm.

such as *Arene tricarinata*, medium trochospiral forms, such as *Tricolia* (16), *Littorina* (28), *Assiminea* (33) and rissoids, long trochospiral forms such as *Finella* (46) and *Diastoma* are found as well as fusiform shells in *Mitrella* and *Anachis* (96, 87), globular shell in *Rissoella* and turrid shapes such as *Nassarina* and *Aesopus*, or marginellid ones like *Olivella* (115, 113) or deviating shapes such as in *Caecum* (35).

A small size and a certain place in the littoral are not necessarily correlated. Gastropods with shells smaller than 5 mm are absent only above the intertidal zone.

Gastropods with shells larger than 50 mm are not found above the eulittoral either. Once again, shell size and shell morphology are not correlated. Fig. 42 presents a few species with a shell that is larger then 100 mm. Among the species with shells larger than 50 mm limpet-like shapes are developed in *Purpura* and *Melongena* (100), low trochospiral shape is found in *Cittarium* with a smooth conch, in *Astraea* (13) with a spiny shell and *Xenophora* with a shell that has encorporated foreign particles. Globulous forms are present in *Tonna* (70); normal trochospires are found in *Thais haemastoma* and *Charonia* (74); fusiform shape is found in *Fasciolaria* (107), *Turbinella* (109), *Latirus* and *Polystira;* conoid shapes are seen in juvenile *Strombus* as well as *Vasum, Voluta, Conus* and *Cassis* (68), with smooth shells like *Conus,* spiny ones like *Vasum,* or with flattened ventral side like

Cassis; a narrow apical angle in the long shell is present in *Turritella,* as well as in *Terebra taurinus* (123); the spire is covered by the last whorl in *Cypraea* and almost covered in *Cypraecassis.* Flaring lips as in *Strombus* (58), varices as in *Murex* and bright colour spots and patterns as in *Conus, Cypraea, Murex pomum* and others are to be found.

The feeding habits in large species vary. *Cittarium* and *Astraea* graze on algae; species of *Cypraea* graze on animals; borers are *Murex, Cassis, Cypraecassis;* snails are present that kill their prey with poison secretions such as *Purpura* do or by injecting poison through hollow teeth as is done by *Conus* and *Terebra. Tonna* and *Charonia* swallow the prey whole, *Fasciolaria, Melongena* and *Turbinella* eat is bite by bite; particles are collected from the sediment by *Strombus* and *Xenophora* and filtered from the water by *Turritella.* But all this is not correlated to shell shape.

Seen from a systematic angle, trochospiral archaeogastropod genera like *Cittarium, Tegula, Calliostoma, Arene, Turbo, Astraea* and *Tricolia* are of a variety of shapes ranging from almost planispiral shell in *Arene tricarinata,* to intermediate forms with flat umbilical region in *Tegula* and *Astraea,* rounded forms as in *Cittarium,* conical-triangular shells as *Calliostoma* has, and fairly high-spired ones

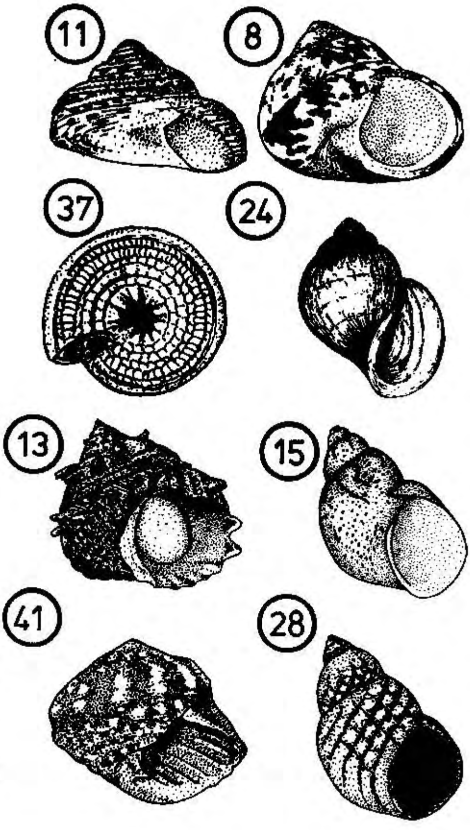

Fig. 43. Compilation of "archaeopod-like" trochospiral conchs.

Abb. 43. Zusammenstellung von Gehäusen mit „archäopodentypischem" Aussehen.

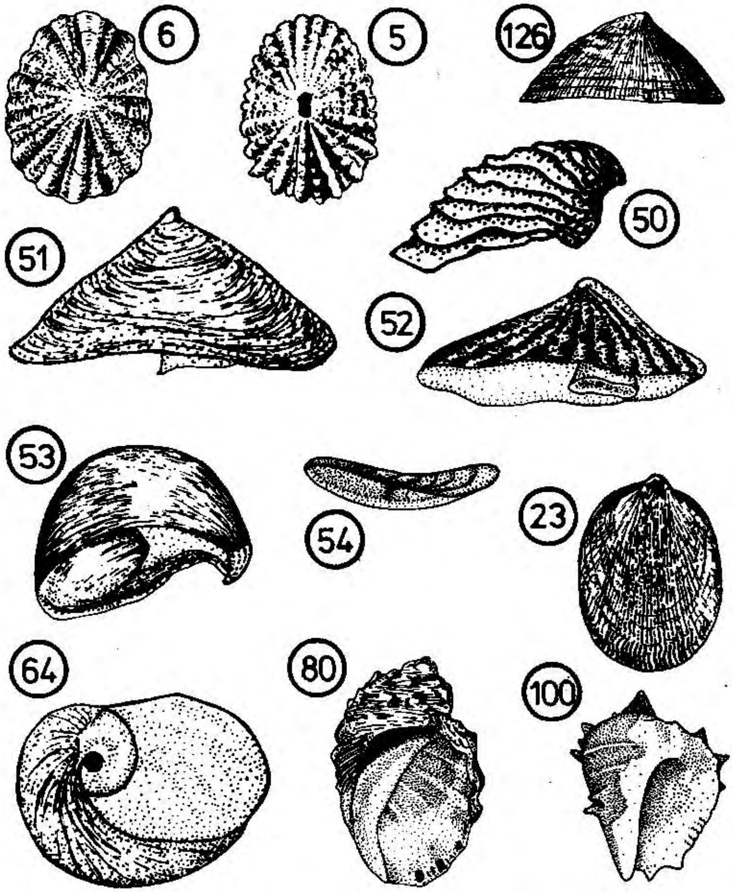

Fig. 44. Limpet-like conchs of different gastropods.

Abb. 44. Napfgehäuse verschiedener Schnecken-Typen.

as found in *Tricolia.* With exception of the last mentioned most of the shells have more or less typical "archaeogastropod" shape, which, nevertheless, can easily be confused with some forms found in higher gastropods. In Fig. 43, *Tegula lividomaculata* (11), *Cittarium pica* (8), *Astraea caelata* (13) and *Tricolia affinis* (15) represent the archaeogastropods, while similar mesogastropods are represented by *Architectonica nobilis* (37), *Modulus modulus* (41), *Littorina meleagris* (28) and *Ampullarius porphyrostomus* (24). Three types of limpets (Fig. 44) can be differentiated. The first category unites cap-like shells with a slit, the second consists of simple caps, and the third of cap-like shells with an internal shelf or sheet. *Hemitoma octoradiata* (6) intermediates between type one and two as an exceptional fissurellid with only a rudimentary trace of a slit. The internal shelf can help to separate archaeogastropod limpets from mesogastropod limpets, but *Hipponix antiquatus* (50) is an exception here and has a smooth interior. In addition the pulmonate limpets *Siphonaria* (126) and the small *Unancylus,* a fresh water limpet that may come into the sea attached to drifting water hyacinths, have simple cap-like shells. Much convergence is thus found in gastropod limpets, which are similar in their reaction to disturbance. In contrast to other gastropods, that retract into their shell and close the aperture with an operculum, limpets have lost their operculum in some stage of their ontogeny (with exception of *Unancylus* where the operculum is eliminated from the ontogeny) and pull their shells to the substrate to which they are anchored with their broad feet. When disturbed limpets, such as chitons, cling to their holdfast and do not fall. However, this reaction may not only be found in gastropods with a cap-like shell, but is also seen in species such as *Purpura patula, Thais deltoidea, T. haemastoma* and even *Nitidella laevigata* with its narrow aperture. *Nitidella* can anchor itself so firmly to *Sargassum* that a tough thallus of this algae is torn and the gastropod in not pulled from its holdfast. *Purpura patula* (80) has a shell that is intermediate in shape between trochospirally coiled gastropods and limpets. It will cling to the rock, but can also close its aperture with a large operculum. Similar shapes are found among gastropods that live in and on soft sediment, such as *Sinum perspectivum* (64) and *Melongena melongena* (100) which close their large aperture with an operculum when disturbed.

Substrate and food preferrences of limpets are quite varied. Species of *Fissurella, Hemitoma* (6), *Diodora* (5), *Acmaea, Collisella, Phenacolepas, Siphonaria* and *Unancylus* feed on plants grazed and scraped off rocks, but *Fissurella angusta* and *F. barbadensis* are exceptions as they obtain their food by filter feeding in the same way as the mesogastropod limpets *Cheilea, Hipponix* (50), *Calyptraea* (51), *Crucibulum* (52) and *Crepidula* (53, 54) do. *Lucapinella Emarginula* and *Lucapina* feed on sponge crusts. Only *Hipponix antiquatus* is permanently attached; all others can leave their place of attachement, but filter feeding species will not usually do so. As far as size is concerned, limpets may measure a few mm (*Unancylus, Phenacolepas* and *Collisella* sp.) to up to 40 mm (*Hemitoma*). Mode of development is not uniform: *Hipponix, Crucibulum* and *Unancylus* are the only creatures that crawl when they hatch from their egg capsules; all others are free-swimming on hatching.

Marginellid to conid-shapes connected by a slit-like aperture are found in widely different families of higher gastropods (Fig. 45). Genera such as *Morum, Cassis* (68), *Cypraecassis* (69), *Cypraea* (60), *Cyphoma* (62), *Trivia* (59), *Simnia* (61), *Columbella* (91), *Vexillum* (110), *Vasum* (108), *Oliva* (111), *Olivella* (113-115), *Hyalina* (116), *Prunum* (112), *Marginella, Voluta* (121), *Conus* (120), *Melampus* (125), *Bulla, Haminoea, Atys, Tornatina* and *Cylichnella* can be grouped here. All have a large final whorl covering much or all of the spire, so that it may be totally concealed. Among these are some of torpedo-like, shell shape that belong to species which move within the sand such as *Oliva, Olivella nivea* (114), *Persicula interruptolineata* (117), and *Prunum.* However, others of similar shape move through algal thickets such as *Persicula pulcherrima, Olivella perplexa* (115), *Hyalina, Bulla, Haminoea, Atys, Tornatina* and *Cylichnella.* A very shiny outer shell surface is found in those species which cover their shell with their foot during motion (*Oliva, Olivella, Persicula, Hyalina, Prunum*) regardless of where they live. But such a shiny outer shell layer is also developed in species such as *Cyphoma, Cypraea* and *Trivia* that

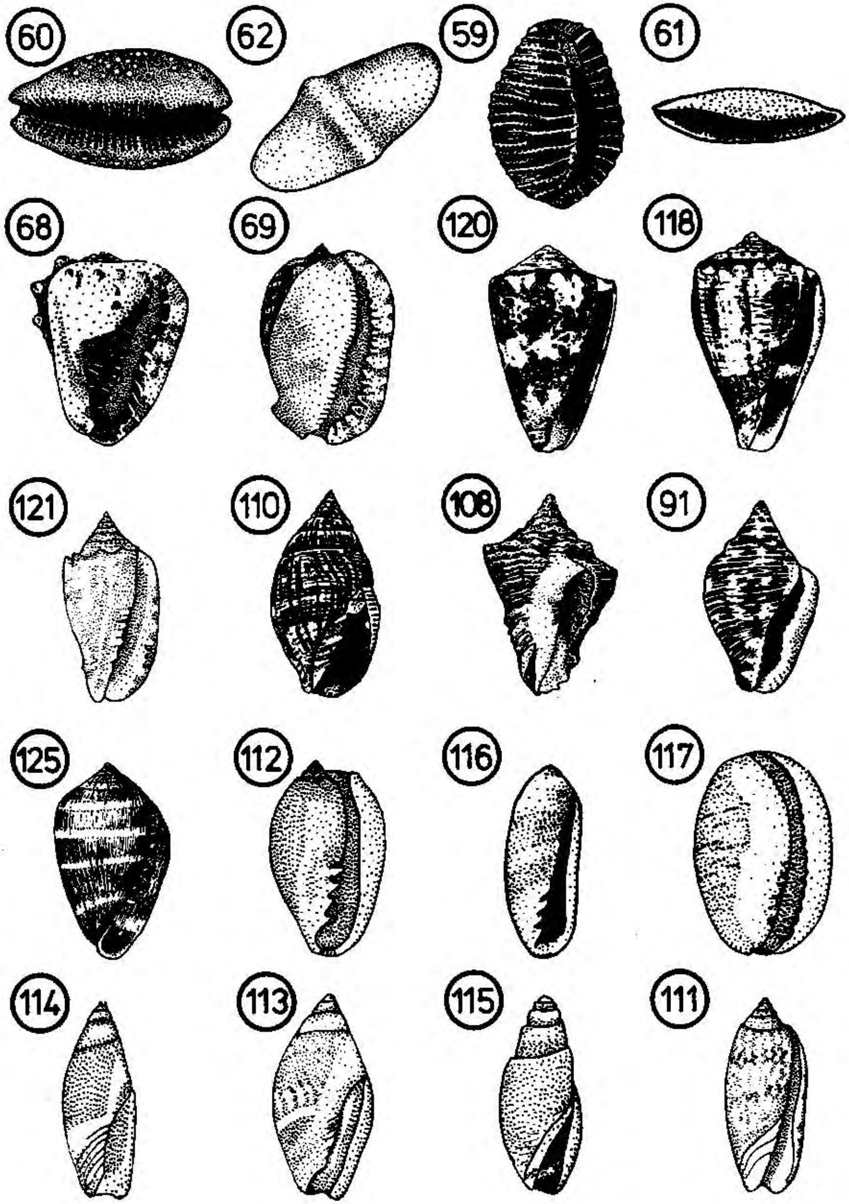

Fig. 45. Marginellid and cone-like conchs of different gastropods.

Abb. 45. Marginellide bzw. conide Gehäuseformen mit schlitzförmiger Mündung von verschiedenen Schneckentypen.

cover the shell with muscular mantle when active. The other gastropods with volutid shape may live on soft and hard substrates, may bury themselves in the sand or remain on the surface most of the time, without these habits being reflected in the shape of the shell. All species with marginellid and conid shell-shape are carnivorous, with only the exception of *Melampus* (125).

Species with a high spire and low apical angle are considered in Fig. 46. Again no correlation of shell shape to a certain substrate or food can be found. *Turritella* (36) lives in mud and is a filter feeder; *Cerithium* (43, 44) collects algal particles on the bottom and on plants; *Diastoma* (45), *Finella* (46) and *Alaba* (48) are microvagous particle collectors; *Cerithiopsis* (47) and *Triphora* (49) feed on sponges; *Epitonium* preys on sea anemones, *Terebra* (123) on worms and pyramidellids and melanellids are parasites on worms and echinoderms. Shell sizes range from minute (*Finella*) to large (*Terebra taurinus*).

A long siphuncular canal is only found among carnivorous species (Fig. 47). Species with such a canal have a long siphuncle; however there are many species with a long siphuncle that have no canal or only a very short one, such as *Nassarius, Oliva, Olivella, Vasum* and *Conus.* Usually species with a long canal such as *Cymatium muricinum* (72), *Cymatium nicobaricum* (71), *Murex brevifrons* (77), *Murex recurvirostris* (75), *Latirus infundibulum* (105), *Latirus angulatus* (106) have a strongly sculptured shell. However others, such as *Turbinella angulifera* (109) and especially *Fasciolaria tulipa* (107) have smooth shells. The presence of a canal gives no clues to the living place and preferred substrate of its carrier. Soft substrate is preferred by *Murex recurvirostris* as well as by *Polystira albida,* hard substrates by *Murex brevifrons, Aspella* and *Favartia.*

A spiny shell may also be found on non-siphonate forms such as *Astraea* (13), *Cenchritis* (32), *Purpura* or *Melongena* (100). Here again substrate preferrence is not correlated to presence or absence of spines or tubercules. In regard to shell thickness, the same can be stated. Extremely thick shells are found in sand-dwelling *Strombus gigas,* rubble preferring *Vasum muricatum,* rock-cliff living *Cittarium pica* and *Thais deltoidea* and muddy-sand preferring *Terebra taurinus.*

Families and groups of species or genera sometimes have certain habits in common. Neritids and littorinids, for example, have characteristic belt-bound species and the largest forms live highest up on the shore. *Nerita peloronta, Chenchritis muricatus,* and *Littorina angulifera* are the biggest and go highest in the supralittoral. Intermediate forms are *Nerita versicolor, N. fulgurans, Nodilittorina tuberculata, N. interrupta, N. ziczac* and *Littorina nebulosa.* In the intertidal zone and just below it, the smallest species such as *Littorina meleagris* and *Nerita tessellata* are found. Vermeij (1974) thought that this increase in size toward the suppermost zones of the shore indicated a general rule; however, caution is advisable here. Juveniles of all species live below water and the rule can only be applied to the rocky shore and only to members of these two families. *Leucozonia ocellata,* for example, which lives in the intertidal zone and above *L. nassa* is the smaller of the two related species.

Not all neritaceans can be used as zone indicators, *Phenacolepas* and *Smaragdia* only occur in sea grass areas, and both deviate from the usual neritacean shell-shape. The shape of the littorinid shell is rather commonly found among archaeogastropods (*Tricolia*) and mesogastropods (rissoids, hydrobiids) and are not much use as indicaters of taxonomic units in fossil assemblages.

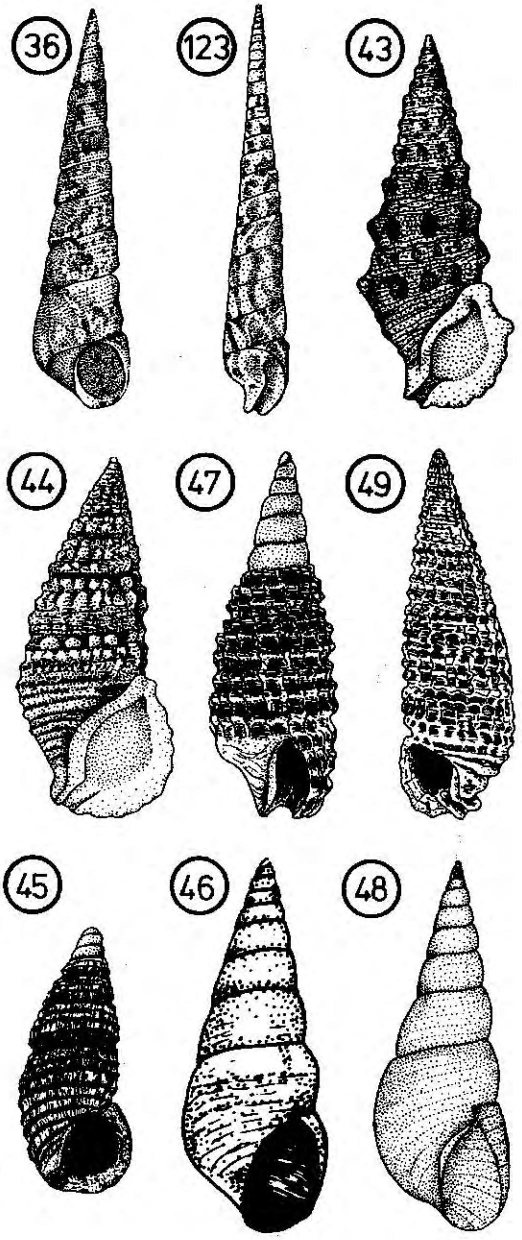

Fig. 46. Gastropod species with a slender, high-spired conch.

Abb. 46. Schneckenarten mit schlankem, hochtürmigem Gehäuse.

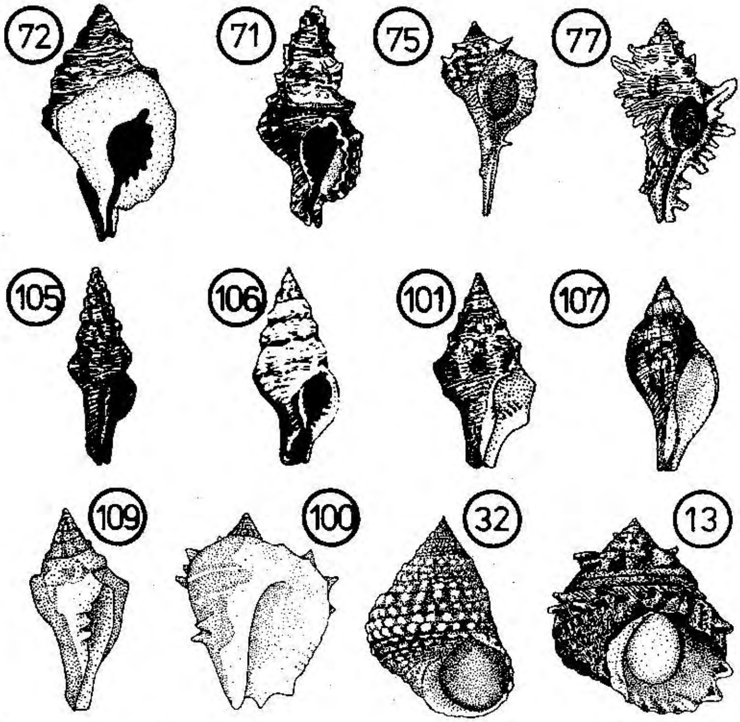

Fig. 47. Gastropod conchs with a long sipho and conchs with spiny shell.

Abb. 47. Schneckengehäuse mit langem Sipho und Gehäuse mit Stacheln.

Muricids encountered in the Caribbean Sea are basically all bivalve and barnacle feeding animals. The only exception is *Coralliophila;* however, its systematic relation to the muricids is not very clear in any case. *Purpura* is a special case here in that it applies the muricid secretion (tyrenian purple) to detach and kill gastropods of the lowest most supralittoral. The neogastropods in general are usually carnivorous, and different species hunt different groups of invertebrates. However, once again species such as *Nitidella laevigata, Columbella mercatoria* and perhaps also *Nassarius vibex* break this rule and live on algae or are omnivorous.

A certain mode of feeding such as filter feeding or parasitizing is not reflected in the shell shape. Filter feeders such as *Turritella, Petaloconchus, Fissurella angusta,* mesogastropod limpets have very little in common apart from their mode of feeding. Parasites as are found in the pyramidellids, melanellids, triphoriids, cerithiopsids and coralliophilids look all different and do not differ much from non-parasitic species either. When a very specific sediment, such as loose sand, is the environment for gastropods movement within the sand is quite uniform. Snails plow through sand with their propodium and cover the shell with their foot. Shells are shiny on the outside, but otherwise may look quite different, as is evident when naticids are compared with olivids. The same type of movement may also be used in other substrates, such as algal thickets.

Coloration of the shell may be hidden under crusts of algae or other epithytes, as is the case in many rock dwelling gastropods of the upper sublittoral. *Vasum muricatum*, *Strombus gigas* and *Turbinella angulata* may carry small coral "reefs" on their shell, which are a good camouflage in a coral rich environment. Others, such as *Xenophora,* produce the same effect by agglutinating foreign particles into the shell, so that it looks like a pile of rubble. Populations of *Engoniophos unicinctus* and *Ocenebra* sp. often show a clear selection of colour morphs on substrates with different composition. Light, white sand or rubble is settled on by populations with a white or light gray periostracum, and dark substrate by populations with brown or dark gray periostracum. Young emerging from the egg capsules show both colorations. In *Persicula interruptolineata* the same selection was observed, but here the coloration is that of the side-parts of the foot that covers the shell. In these three species, the effect of predation by molluscivorous animals that hunt with the aid of their eyes (crabs, fish) on the colour composition of a population is evident.

Camouflaging by coloration and selection of non fitting colour morphs can also be observed in other gastropod species, as in *Neritina virginea* and *Phyllaplysia engeli.* The first shows a very wide variety in colorations of the shell when grown in the aquarium, while in the field only colour patterns that merge with the substrate survive. The second is brown on a brown background (*Sargassum*) and green on a green substrate (*Thalassia*). The opposite of camouflage is the use of warning colouration as is present in some opisthobranchs such as *Spurilla, Phidiana, Flabellina* and *Dondice.* These naked opisthobranchs that feed on coelenterates are poisonous.

In many gastropods coloration is not a very important factor in selection because they are nocturnal in their habits and hide within the sediment or under rocks during day.

Hydroidea.

Hydroids are organized in two totally different ways. Most species produce an elastic skeleton, few species such as the milleporans secrete a calcareous non-flexible skeleton.

Colonial coelenterates (e. g. hydroids) aquire an ideal shape when they can grow without environmental pressures produced by the hydrodynamic conditions and by competition of other benthos. Species with an elastic skeleton, such as *Eudendrium carneum* or *Cnidoscyphus marginatus,* under normal conditions, only in deep water form colonies of nearly ideal morphology. Where similar coditions are present in shallow water, as is found below the concrete structure of the harbour jetty; colonies with nearly perfect shape can also grow. Algal competion is absent here and currents are moderate and stable. The shape of a coelenterate colony like hydroids is closely correlated to the motion of water. Strong movements of water produce broad crust-like, low colonies, quiet water leads to spherical, high colonies.

Hydroid colonies in themselves show a number of characteristic growth types which are related to their systematic place. Many Campanulariidae, for example, are of grass-like shape, most Plumulariidae are feather-like in shape and Eudendridae are of tree-like composition. The grass-like type shows no adaptation to the physical environment apart from size. Feather-like hydroids grow so that their largest surface is vertical to dominant current direction. Feather-like hydroids such as *Aglaophenia latecarinata* and *Plumularia setacea* grow in small niches, cavities and channels in the rock within the turbulent zone. The generally non directed turbulent wave motion is channelled into directed current in these small depressions and swings back and fourth. The small plumulariid hydroids of the lower surf zone need this periodical up and down for their development in a small scale and are not found in areas with only unidirectional currents.

Below the zone of turbulent and oscillating currents unidirectional currents usually prevail. Bilaterally flattened feather-like colonies of different species of *Sertularella* are common here and are always vertical to current direction. Thus, in the orientation of their colonies *Sertularella* species faithfully reflect the direction of the main current stream in a rocky littoral. Feather-like hydroids such as *Lytocarpus (Aglaophenia) allmani* and *Lytocarpus philippinus* grow in quieter deeper water in such a way that their colonies are highly branched and aquire spherical appearence.

Millepora has a calcareous rigid skeleton and only lives in shallow water. *Millepora complanata* f. *squarrosa* produces its compact irregulary folded crusts and solid sheets under shallowest conditions in the uppermost sublittoral. It is quite resistant to surf and, therefore, composes the top of reefs together with calcareous algae. *Millepora complanata* lives below the surf zone and constructs colonies formed like walls which are oriented mostly parallel to the main current, in contrast to the feather-like hydroids, which are usually oriented vertical to current direction. *Millepora alcicornis* lives around 3 m depth downwards and produces colonies of a tree-like shape. Branches are somewhat compressed and larger branch surfaces are oriented vertical to the direction of the current.

All three types of *Millepora* are variable in the morphology of their colonies (Fig. 5). *Millepora* may encrust dead gorgonians and reflect the shape of the skeleton of its substrate. The outcome is for example a *Millepora* with the morphology of a *Gorgonia ventalina*. However, *Millepora* may only use the main skeletal axes of *Gorgonia* as a substrate; in this case, the result is a planar wide meshwork of quite different morphology. *Millepora complata* is especially common on the lagoonal slope of the coral reefs. Its colonies grow in a wide variety of shapes as well as in the usual sheets. In areas with turbulent water or not directed currents, sheets may be bent or twisted and thin. The opposite is also possible and massive colonies with a pyramidal cross section can grow.

Reproduction and Growth in Relation to Environment.

Gastropoda and Polyplacophora.

Gastropods and chitons of the tropical Caribbean Sea follow three strategies of reproduction. The most simple is to drop eggs and sperm in seawater where fertilization occurs. This is the case with most members of the archaeogastropods and polyplacophores. To increase the success of the process, males and females assemble in large groups or at least with one member of each sex before eggs and sperm are released. Eggs develop while drifting in the water or sink to the bottom were they remain until swimming larva hatch after about 2-4 days. The larva may swim for several days without feeding. They rely on the energy of their egg-yolk until they settle and take up benthic life (BANDEL 1982).

The second method of reproduction is that of planktotrophic larvae hatching from egg capsules. Fertilization in all higher gastropods including the neritaceans is internal, and egg masses or capsules are attached to the substrate, brooded or released in the water. Development within the egg capsule is variable and connected to the species place in the natural system. *Strombus gigas*, for example, will hatch after 4 days development, *Thais haemastoma* after 25 days and *Latirus infundibulum* after 45 days. The veliger larva feeds on minute planktonic organisms and remains swimming freely in the sea for a few days to a year's time. The length of the stay in the plankton is characteristic to the species and not correlated with the place of the species in the littoral environment or in the system of classification. When the larva is transformed into the benthic snail it has to perform a true metamorphosis with reconstruction and replacement of a number of organs and the begin of a totally different life with completely new requirements of feeding.

The third method of reproduction is derived from the second. In it, the larval phase occurs within the shelter of an egg capsule and planktonic feeding is substituted by yolk feeding or nurse egg feeding. The young hatch as miniature adults and there is no free-swimming larval phase within the life cycle. Several species intermediate between method 2 and 3. The intermediating individuals may either produce eggs from which crawling young emerge or from which pediveligers hatch; the pediveligers can still swimm for a while, but do not usually feed while swimming. In most marine gastropods the process of free veliger development and development within the egg capsule is reversable in transition from species to species and sometimes even within a species.

Most of the gastropods and chitons considered here produce offspring at all times of the year. The only two species encountered with a single spawning period within a years time are *Turritella variegata* and *Turbinella angulata*. *Turritella* individuals of a whole population leave their hiding place in the sediment once a year to copulate and spawn, afterwards they return into their normal position within the mud and sand and continue filter feeding (BANDEL 1976). *Turbinella* females form one very large egg mass each year from which large young emerge after an extended embryonic development within the string of egg capsules of over 100 days (BANDEL 1975). This growth to almost 10 mm size is possible because each individual devours several thousand nurse eggs.

Explosive increase of individual numbers in a population is usually connected to the appearance of a new environment. It can occur almost as rapidly with pelagic non feeding larvae as with planktotrophic larvae or with young hatching as crawling miniture aduls. The archaeogastropod *Tricolia affinis affinis* is a case of the first category and occurs rapidly in large numbers wherever *Sargassum* grows on a rocky shore. *Alaba incerta* also appears here, representing the second case, coming to the algae via long term planktonic veliger. *Nitidella laevigata* arrives at the same substrate as short term planktotrophic veliger. Similar rapid arrival from planktotrophic larvae is found in the case of the mangrove snails *Neritina* and *Melampus.* They can usually only reach their estuarine or lagoonal living place with exceptionally high floods. More cases of rapid settling by feeding veligers on algae are found in the opisthobranchs *Bulla, Haminoea, Elysia, Aplysia, Phyllaplysia,* and *Bursatella.* Newly grown food organisms such as sea anemones and sponges, as are found in the rare periods when the Cienaga Grande lagoon reaches or exceeds normal marine salinity, are found by the pelagic larvae of *Epitonium* and *Cerithiopsis* which establish large populations.

The third case of population explosion occurs when floods turn the Cienaga Grande lagoon into a fresh water lake. *Assiminea succinea* populations establish themselves and increase rapidly in number. Many eggs are continuously produced by *Assiminea* and young hatch after only one week of development. Similar population increases occur when crawling young hatch from numerous small capsules on mud and sand as is the case with *Ocenebra* sp. and *Olivella perplexa* which have an embryonic development of less than 10 days (Bandel 1975, 1976). Special substrates (e. g. a beach with fresh water moving through it) are populated quite rapidly by *Terebra cinerea,* even though the young need 30 days before they hatch. Hatchlings here have a very high chance of survival; they emerge from capsules that are attached to adult individuals of the same species sheltered within sand and surrounded by plenty of food. The case is similar in *Conus jaspideus:* It settles in a lagoon that has returned to normal salinity after a brackish period. As in *Tridachia cristata,* large populations are established rapidly here, even though embryonic development lasts 14 days.

Occurrence and mode of hatching are not correlated, with perhaps one small exception found among the high supratidal littorinids, *Cenchritis muricatus* and *Littorina angulifera.* Both release veligers when in normal sea water. The other littorinids produce egg capsules and supratidal *Nerita* move to the lower intertidal zone, where they attach their egg cases. Size and numbers of individuals in a population are not correlated either; however, the space occupied by a single population may differs. A population of the small *Atys riiseanus* may be limited to a few square meters of algal covered mud and may consist of as many individuals as the population of the sea hares *Aplysia* that settle in the shallow water of a whole portion of a bay. As a general rule, a square meter of substrate supports more small gastropods than large ones, but small species, for example *Arene* and *Aspella,* may occur in small numbers just like some big ones such as many species of *Conus.*

Reproduction can be an almost continuous process spread over all periods of the year. Spawn of most species is encountered at all times, but its production may be discontinuous and connected to the avalability of food. If *Bursa, Cymatium* or *Murex* find an abundance of food, they produce several egg masses each year; if food is scarce, only a few are produced. A well fed *Bursa,* for example, produces an egg mass and broods on it for 10 days until veligers hatch. During this time it does not feed. When feeding conditions are optimal, as in aquarium populations after only one week of feeding the female may begin to produce the next spawn.

Brooding of egg masses is a common among gastropods. *Littorina angulifera, Chenchritis muricatus* as well as *Planaxis* keep brooded young in their mantle cavity, *Petaloconchus* and all mesogastropod limpets protect spawn in their shell until young hatch, *Coralliophila, Thais deltoidea* and *Purpura patula* hold egg capsules in the pallial cavity until young hatch and *Charonia, Bursa* and *Cymatium* brood egg masses and keep them well aerated until veligers hatch. However, once again brooding is not correlated to the living environment.

The time spent as a larva is not correlated to the place of the adult in the littoral or to its place in the system either. Such different species as *Smaragdia viridis, Alaba incerta,* species of *Cerithiopsis, Seila* and *Triphora, Architectonica nobilis, Epitonium lamellosum, Simnia aciculata, Cyphoma gibbosum,* species of *Cypraea* and most tonnaceans, thaidids, *Mitra* and most species of the turrids spend several months in the plankton. Most others that hatch as veligers remain free swimming and feed on plankton for a few weeks. Size of the embryonic shell, i. e. the shell carried by the veliger when it hatches from the egg, is related to the place of its producer within the natural system (0.1 to 0.9 mm) (BANDEL 1975). Size of the larval shell is characteristic to the species and may range between 0.2 and 5 mm.

Archaeogastropods on chitons settle down after short swimming period of a few days. About 90% of all mesogastropods (including neritaceans) hatch as veligers and about 50% of neogastropods hatch free swimming. All opisthobranchs with exception of *Tridachia crispata* hatch as veligers (BANDEL, 1976), like the two marine pulmonates. In opisthobranches all nudibranchs discart their larval and embryonic shell after completion of the larval veliger phase.

After metamorphosis most gastropods pass through a stage of minute size. Exceptions are found in Tonnacea, where freshly settled young may have veliger shells of up to 5 mm in size (BANDEL, 1981), and in species that feed on nurse eggs during their embryonic development or have much yolk.

Murex brevifrons, Fasciolaria tulipa and *Turbinella angulata* with 5-10 mm conch-length are such cases. Most of the others begin their benthic life with a shell smaller than 1 mm, often considerably smaller as is the case in all archaeogastropods. Young individuals and adults often live at different places. With exception of *Littorina meleagris* all other littorinids grow up in tidal pools or spray pools or within the infralittoral fringe. They can only expose themselves to dessication and heat after having reached a shell size of about 3 mm. In the case of *Cenchritis* and *Nodilittorina* conditions for the establishment of new populations occur only at certain times of the year and in might not occur at all in some years. Algal thickets below low tide line represent the nursing environment for the young of many species such as *Fissurella nodosa, F. angusta,* the species of *Nerita, Chiton* and *Acanthopleura.* Dense populations of mussels in the intertidal zone give shelter and food to the young of *Leucozonia nassa, L. ocellata, Thais deltoidea, Purpura patula, Morula nodulosa* and *Thais haemastoma.*

In the case of the fissurellis, young specimens have a shell resembling that of *Scissurella* for a certain time of their life before they become limpets. Like *Scissurella,* they move through algal thickets. Strombids can climb vertical walls when they are young and hide within algal tufts and among rocks. Before the flaring lip of the adult is formed, *Strombus pugilis* lives outside of its normal sea grass environment among algal covers and hard substrates, its shell covered by algae. When adult, the shell is cleaned from algae and the population moves into the sand flats. Here not a single juvenile may be encountered within a population of many thousands of adult individuals.

Other gastropod species may be present in all ranges in the same location. This is, for example, the case with all gastropods living on *Sargassum* but also with *Cittarium pica, Littorina meleagris, Petaloconchus varians* on rocks, *Modulus modulus, Cerithium lutosum* in the lagoon, *Crepidula convexa* and *Crepidula plana* on gastropod shells, *Triphora, Cerithiopsis, Seila, Coralliophila, Cingulina* on their hosts and many others more.

Young individuals of a species may look like or similar to the adult as, for example, in *Cittarium, Tegula, Littorina, Cerithium, Ocenebra* and *Terebra;* or they may look quite different from the adult. A young *Strombus* looks like a slender cone and lacks the characteristic outer lip of the adults. Young *Cyphoma, Trivia* and *Cypraea* look more like a *Simnia* and have thin walls and may show the spire. Later the spire is covered by the last whorl and shell wall is thickened. Similar changes between thin shelled young and thick shelled adults are found in some marginellid neogastropods. The change from the openly coiled early juvenile shell of *Caecum* and the later elephant tusk-like adult shell is quite drastic but usually no longer visible because the early shell breakes off and the apical end is formed by a septum.

Representatives of different species may have a different life-span. *Aplysia,* for example, reaches full size and maturity within a few months. After spawning the large slugs die. *Strombus gigas,* in contrast, will live for many years and extremely old individuals, that thickened the shell from within continuously while the outside became corroded, turn into "*Strombus samba*". These heavy, smaller individuals of *S. gigas* are probably quite a bit older than 10 years. Other gastropods of similar age are *Cittarium pica, Cenchritis muricatus, Charonia variegata, Turbinella angulata, Vasum muricatum* and *Terebra taurinus.* But also smaller forms like *Neritina virginea* may get quite old. Individuals of this species were held in a small aquarium for 7 years and only died when the aquarium broke. Houbrick (1974) expressed the opinion that *Cerithium* has a life span of about one year. This may commonly be so in nature, but in the aquarium Mediterranean species of *Cerithium* and *Batillaria minima* from Bermuda were kept alive for more than two years.

No general statements can be made regarding life span of a marine gastropod. Many small species like *Alaba, Finella, Diastoma, Tricolia, Caecum* and *Persicula* probably do not live a long time. But how old a *Triphora* or a *Nassarius* may get has to be shown by the experiment.

Schäfer (1962) thought that among gastropods death due to old age is the usual. But this statement can not be confirmed in the tropical fauna. Gastropods living in soft sediment have a very high chance to be killed by naticids, muricids or *Oliva.* Only big and thick-shelles adults can be considered fairly safe. The chance of most gastropods to die before becoming old and adult are very high. Many populations, therefore, consist of adult individuals only when they are less vulnerable to attack or environmental stresses.

Hydroidea.

Tropical colonial coelenterates, in general, have specific periods of reproduction and do not produce off-springs at all times of the year. But periods of reproduction within the same species of populations that live in different environments and in geographically separated areas may not be in phase with each other. The plankton will hold medusae and planulae at all times of the year even for such species that produce medusae and planulae only once during one years time. Examples are *Filelum serratum* for planula and both species of *Hebella* for medusae. *Halocordyle disticha*, in contrast, represents an exception to periodic reproduction and produces medusae continuously.

Planulae of many hydroids remain in the plankton long enough to be able to cover large distances and even to cross the Atlantic Ocean. Their size ranges between 0.2 and 0.8 mm and they remain swimming for more than 4 weeks. Planulae float and actively remain within a certain body of water swimming with cilia. Many planulae, in addition, produce mucus threads that help them to remain floating.

Even though planulae may stay alive in the plankton for such a long time, there are many species that produce planulae either by internal (sporosac) or free medusa phase, where planulae can attach themselves to a favourable substrate and grow up to form a polyp within the same day of their hatching from the gonophore. If the substrate is not quite satisfactory the planula may crawl about in search for a better place for final attachment. If no favourable substrate is available the same planula remains free swimming in the plankton. Chemical stimulants can attract planulae like those of *Clytia simplex* are attracted to *Sargassum*.

Medusae probably survive within a moving body of water for a considerable length of time comparable to that of the planulae. Their size ranges between less than 1 mm and almost 10 mm and is species specific. Medusae mainly drift, but they can follow migrations of planktonic organisms that compose their food by own jet propulsion swimming. Medusae of *Verticellina* sp. from the Cienaga Grande where kept alive in the aquarium for 4 weeks without reaching maturity.

Primitive hydroids like *Sarsis eximia* or *Halocordyle disticha* generally tend to have planktonic medusae. Phylogenetically more advanced hydroids like *Cladocoryne pelagica* have reduced medusae that no longer become independent from the colony and remain attached (sporosac). Intermediate forms like *Zyzzysus solitarius* are sporosac but here the medusa forms almost to completion but does not detach itself from the colony (cryptomedusoid stage). Medusae are also usually present when polyps settle extreme conditions as for example within the surf zone on short lived algae. Such cases are found in *Sarsis* spec., *Obelia geniculata* or small sized hydroids which live on other, larger hydroids, like *Obelia dichotoma* and *O. bidentata*. Also forms like *Halocordyle disticha*, which lives in strong competition with algae, produce medusae.

Even though the general trend of medusa formation in stressed environments can be noted there are many exceptions to be stated. *Campanularia lennoxensis* and *Dynamena quadridenta* for example live on short lived algal substrate but have sporasacs. *Millepora* produces medusae which do not feed while free swimming and, therefore, have to reproduce within a very short time.

Colonial organisms after first attachment to a hard substrate or any later phase of growth may, under favourable conditions form special vegetative types of reproduction. The polyps bud and these buds migrate away from other polyps by amoeboid movement, completely separating themselves from the mother animal. In this way a favourable area can be settled quite rapidly.

When conditions become unfavourable the polyps of a colony may produce buds in the same way and these buds are transported by the currents without the possibility of own locomotion. In this way a settlement occurs in a purely statistical and chance manner and no choice of the place of attachment and new establishment of the daughter colonies is possible. Vegetative reproduction in the way of independent buds is a feature that is generally found among coelenterates. The normal enlargement of a colony of hydroids is by growth of root-like stolons from which new polyps and thus new cormi grow. Similar growth can be noted in octocarallians as well as among tunicates.

A further mode of vegetative reproduction in reaction to a newly available substrate is observed in species like *Cnidoscyphus marginatus, Halopteris diaphana* and *Aglaophenia* sp. Colonies of these grow hook-like stolones on terminal parts of branches at those portions of the colony where it comes in touch with an opposing substrate. When *Cnidoscyphus,* for example, grows to such size that branches of the colony during their motion in the currents of the water come in touch with an opposing hard substrate like a pillar below the jetty, or when *Halopteris* growing on a rock surface is touched by *Sagassum* weed swaying in the surf, the hook like stolons attach themselves to the new substrate and are torn off from the mother colony. They then grow into new colonies by themselves. This type of new settlement is characteristic for species in zones with strong water motion.

Within the estuarine area or under conditions of the brackish lagoon the living environment may periodically deteriorate to such a degree that a biocoenosis is totally wiped out. *Garveia cerulea* can survive such periods. The soft body withdraws from the cormi and migrates into the root-like stolons, which are closed by the perisarc (external skeletal wall). Here the animal survives until brackish water conditions are reestablished. Only this species has such an encapsulated stage.

The Zonation in the Santa Marta Area.

Zonation of the littoral is basilically caused by two abiotic factors: These are water movement and light/heat. Strongly exposed shores have a wet zone from wave spray and splashes that is much wider than the wet zone of protected shores. In protected shores only the narrow intertidal zone may become periodically damp during high tides. Faunal belts on the rocky exposed shore are, therefore, much wider than on protected shores. At the times of the year that strong trade winds blow, the waves are high, the spray reaches relatively high points and the wave base is low. At rainy times, when quiet conditions prevail, the damp supratidal zone is much narrower and the well oxygenated subtidal zones reach a lesser depth. The alternating position of the sun exposes the zones of the shore to light and heat changes throughout the day. During the course of the year they are influenced by the change from dry clear weather when the breezes blow and by cloudy skies during rainy times when trade winds have calmed down.

Of the animal and plant life of the shores, mollusks and coelenterates reflect these abiotic factors by taking their place on and in the substrate and by interacting with each other. Due to the growth of organisms, other organisms get a chance to find suitable substrates. Thus, the abiotic conditions are moderated by the biological reaction to them. It is thus clear that when any factor changes, belts of similar fauna and flora move up and down the shore or disappear totally. Due to the interruption of current-force by artificial constructions in the harbour of Santa Marta, for example, the number of individuals of the spiny sea urchin *Diadema antillarum* has increased since 1972 at the southern shore of Punta de Betin and resulted in a total disappearance of the Sargassum in the sublittoral fringe. Along with that alga the varied fauna that lived on it also disappeared. Actually (since 1984) *Diadema antillarum* had disappeared due to a sudden total mortality. The effect of this event will be very interesting.

Gastropoda and Amphineura.

Gastropods may show different tendencies regarding their occurrence within the littoral zones. Some can be found in a certain depth and on a definite kind of beach. Among these we find *Hemitoma octoradiata, Fissurella nodosa, F. angusta, F. nimbosa, Cittarium pica,* the species of *Tegula, Astraea caelata,* all *Nerita* and *Neritina* species, the littoinids, *Petaloconchus varians, Planaxis sulcatus, P. nucleus, Cerithium lutosum,* the species of *Strombus, Polinices lacteus, Sinum perspectivum, Morula nodulosa, Purpura patula,* the species of *Thais, Columbella mercatoria, Anachis brasiliana, A. pulchella, A. sparsa, Nitidella nitida, Mitrella ocellata, Engina turbinella, Pisania pusia, P. tincta, Engoniophos unicinctus, Nassarius vibex, Leucozonia nassa, L. ocellata, Vexillum puella, Terebra cinerea, Melampus coffeus* and *Siphonaria pectinata.* All these species faithfully reflect a certain area within the littoral zones and a specific place and substrate. Of the chitons the two species of *Chiton* and *Acanthopleura granulata* can be added to this list.

Other species are bound to a living substrate. *Sargassum,* for example, is settled on by *Tricolia affinis affinis, Alaba incerta, Nitidella laevigata, Mitrella argus, Phyllaplysia engeli, Scyllae pelagica, Stylocheilus longicauda* and *Elysia ornata.*

Outside of this environment, individuals belonging to these species are usually quite rare or absent.

Dense thickets of filamentous green algae and moss-like algae on mud, sand or rocky bottom contain a number of gastropods such as different species of *Caecum, Finella dubia, Bulla, Olivella petiolita, O. perplexa, Marginella lavalleana, Persicula pulcherrima, Cylichnella, Atys* and *Tornatina.* Rissoids may also be present, when thickets are in deeper water. Growths of green algae such as *Enteromorpha* and *Ulva* that periodically cover the bottom of quiet portions of the bays are the environment for huge populations of *Diastoma varium,* the bubble shells *Bulla* and *Haminoea,* the sea hares *Aplysia* and the sea cats *Bursatella* and *Dolabrifera.*

Sea grass has its own characteristic gastropod fauna. On the eel grass *Tricolia affinis cruenta* and on the turtle grass *T. bella* are found. Other typical species are *Smaragdia* and the green variety of *Phyllaplysia engeli,* on deeper grass meadows also *Phenacolepas.*

Not only plant substrates but also animal substrates have a characteristic gastropod fauna. *Gorgonia,* for example, is practically always settled on by *Simnia, Cyphoma* and *Coralliophila caribbaea.* Sponges very commonly have members of the genera *Triphora* and *Cerithiopsis* feeding on and inside them. While the algal substrates and *Gorgonia* are limited to a certain depth range and, therefore, also the gastropods living on and in them are limited to these depth zones, sponges no longer follow these rules. *Cerithiopsis* and *Triphora* may be found in the shallow water of the Cienaga Grande as well as at great depth, as long as sponges grow there. These gastropods will spend most of their life within or on one host, while others with similar food requirements move from host to host, from one substrate with food attached to them to the next. Such animals restricted to sponge and tunicate crusts are *Seila, Trivia, Cypraea, Calliostoma, Lucapina, Lucapinella,* and *Emarginula;* coelenterate feeding species like *Architectonica Epitonium, Coralliophila abbreviata, C. aberrans* and aeolid nudibranchs like *Phidiana, Favorinus, Dondice* and *Spurilla* are found wherever their food finds fitting living conditions. Other cases are to be seen in echinoderm feeding species such as *Charonia, Cassis, Cypraecassis* and *Phalium* or worm feeding species such as many members of the Conidae, Terebridae and Turridae.

But also the type of substrate may be of great importance to the occurrence of certain species. *Turritella, Natica livida, Murex recurvirostris, Melongena* and *Oliva scripta* are almost exclusively found in and on muddy bottoms quite independent of their depth. Well sorted sand from intertidal to deep water may be roamed in by *Nassarius albus, Oliva reticularis, Natica canrena, Polinices hepaticus, Persicula interruptelineata* and *Olivella nivea.*

If we look at these three differences regarding gastropod occurrence from a systematic point of view we can note that there are a few groups which are characteristic of a certain zone in the littoral environment. Here *Nerita*-species, *Nodilittorina* species, *Planaxis* species can be mentioned. Others are characteristic of a zone and a specific type of substrate, such as *Tegula* species, *Littorina* species, *Thais* species. From these we can select pairs of very similar gastropod species of which one member may characterize a littoral belt, while the other is of no use for such a purpose. The pairs such as *Fissurella* on the one hand and *Diodora* on the other, with *Collisella antillarum* on the shallow rocky shore, while *Collisella* sp. occurrs bound to *Thalassia; Petaloconchus varians* being characteristic of the intertidal cliff and *P. erectus* connected to *Palythoa* crusts; with *Modulus modulus* bound to reef-lagoons and sandy pebble and *M. carchedonius* to no specific ground; *Cerithium lutosum* characteristic of shallow lagoon and *C. atratum* and *C. litteratum* present wherever food can be found; *Crepidula convexa* attached to living gastropods only in the very shallow water, and *C. plana* found wherever a large hermit crab may carry its home; with *Polinices lacteus* roaming the shallow sand and fine gravel and *Natica canrena* and *Polinices hepaticus* in all sands; with *Morula nodulosa* only in the uppermost sublittoral and *Ocenebra rosea* and O. sp. on hard and soft surfaces in all depth ranges; with *Purpura* and *Thais* in distinct littoral zones and *Murex* without depth preferrence; with columbellids such as *Columbella mercatoria, Nitidella nitida, Mitrella ocellata, Anachis sparsa, A. brasiliana* and *A. pulchella* as good zone indicators and *Nitidella laevigata* and *Mitrella argus* bound to *Sargassum* and *Anachis obesa* and *Mitrella lunata* present wherever hydroids live; *Nassarius vibex* lives near the shore only, while *N. albus* is omnipresent in sand; *Terebra cinerea* occurs high in the sandy shore and *T. taurinus* at all depths; *Drillia solida* lives among rocks in the beach, while other, similar turrids live in soft bottoms of all depths.

Some gastropods found in the sublittoral such as species of *Cerithiopis* and *Triphora, Polinices lacteus, Cypraea cinerea, Nassarius albus, Hyalina avena* and *Polystira albida* have been shown to live also in depths of over 100 m (LEWIS 1965). This clearly shows their dependence on a substrate and a source of food and an almost total independence of water depth.

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