ASPECTS OF LITTORAL LIFE IN THE INDIAN OCEAN (*)

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THE VEGA EXPEDITION

Last year I was invited by the Woods Hole Oceanographic Institution to join the American program of the International Indian Ocean Expedition (IIOE).

The IIOE is a scientific endeavor primarily concerned with obtaining biological, physical, chemical and geological information about the land, ocean and atmosphere in the Indian Ocean.

The ship I was on, the R/S Te Vega is a twomaster which belongs to Stanford University and is well equipped for the investigation of littoral waters down to 30 m. Although there are winches strong enough for dredging operations down to 4000 m we concentrated almost exclusively on the region between high tide level and the depth where reef-building corals begin to disappear. All kinds of collecting and diving gear, aqualungs, underwater cameras and fiberglass skiffs with outboard motors were available, producing efficient and pleasant working conditions.

There is space for 15 crew members and 15 scientists on board; from October to December 1963, when I joined the vessel, we were 5 senior scientists and 7 students, the latter to be our assistants and to get training in marine biology. Dr. R. Bolin, ichthyologist from

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Stanford University was the scientific director, Dr. A. Kohn, University of Washington, studied the distribution and ecology of the poisonous snail genus *Conus,* Dr. J. Rosewater collected mollusks for the US National Museum, Dr. L. Colinvaux worked on systematics and distribution of the algal genus *Halimeda* and I myself was interested in the systematics, ecology and distribution of sponges.

Within the Indian Ocean the Te Vega had to cover its program during 3 cruises with various scientific parties: from Singapore to Colombo, from Colombo to Mauritius and from Mauritius to Zanzibar. Each cruise lasted 3 months, duration and places for stopovers were decided by the scientists in accordance with their requirements.

Our cruise started in Singapore and followed the Westcoast of Malaysia and Thailand where much collecting was done on little frequented islands in the Malacca Straits. Close to the border of Burma we changed course, sailed around the northern tip and south down the West-coast of Sumatra, working on Nias and Mentawai Islands as far as Mega, 4° southern latitude (Fig. 1)

One week before sailing over to Colombo our mainshaft broke and because of lack of wind so close to the equator we had to leave our vessel in Padang, Sumatra.

TROPICAL LITTORAL

The regions of the Pacific

Although there exists — within the region of the shelf — a circumpolar fauna which occurs in both Atlantic and Pacific, the warm-water fauna of the Pacific does not constitute a single unit. Many animal groups such as Anthozoa (*Fungia, Sarcophyton, Isis*), Mollusca (*Hippopus, Tridacna*), decapod Crustacea (*Birgus latro, Palinurus japonicus*), Echinodermata (*Crinoids, Diadema*) and fishes show a distribution from East Africa to Tahiti and the most Eastern Islands of the Pacific, but do not reach the Pacific coast of America. The deep zone in the eastern Pacific seems to form a barrier, which prevents transgression (1). For this reason and because of similarities

(1) As shown by Squires (1959), Ekmans « Eastern Pacific Barrier » does not apply to many reef-building corals.

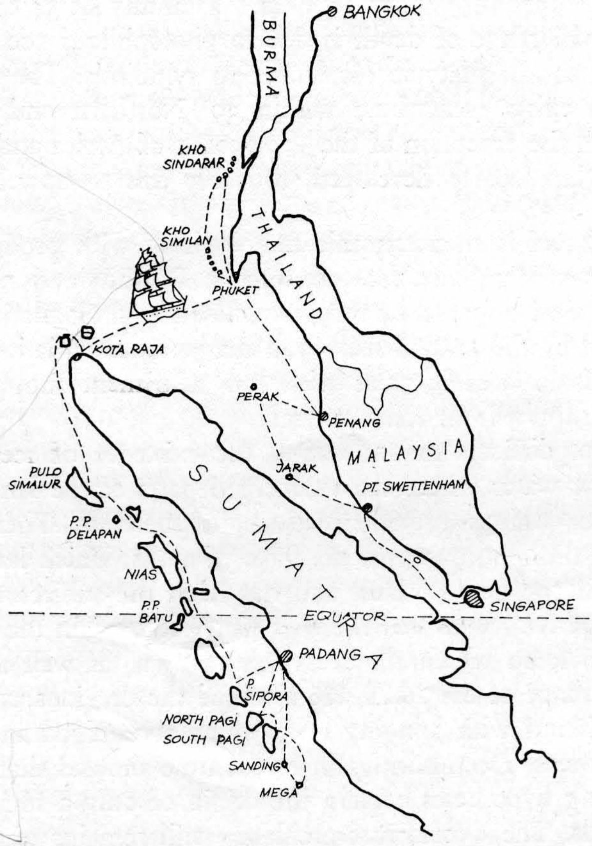

FIG. 1 - The TE VEGA cruise from Singapore to Padang

in the fauna on both sides of the American continent we divide with Ekman (Ekman 1953) the warm-water fauna of the shelf into an Indo West Pacific and an Atlanto East Pacific region. Within the Indo West Pacific region one may distinguish several subregions among which the Indo Malayan region is considered as a faunistic center for most of the species. The further one leaves from this center in any direction the poorer is the fauna. The most western part of this region was the territory of our investigations.

Coral reefs

Occurrence. In the tropics everywhere down to the depth of 50 m reef-building corals flourish whereever there is a suitable substratum, a temperature above 20° C and a salinity of 34 to 36‰.

The small range of depth is due to photophilous zooxanthellae with which the hermatypic corals live in symbiosis. The optimum temperature exists everywhere within 30° Northern and Southern latitude with the exception of the West-coasts of Africa and America where reefs are poorly developed, probably due to upwelling cold water.

A coral reef is an autonomic unit in itself with producers and herbivore as well as carnivore consumers. Benthos and necton are protected against dispersal by relatively closed local circulation which is controlled by the local density and temperature variations. Large organic reefs in oceanic areas with low nutriment supply do not depend on supply from the open sea.

It is not difficult to understand the existence of reefs in tropical shallow water where the submerged parts of the land-mass of continents or islands provide ready-made substrats. There is one type of reef though, mostly in the form of atolls, which has no connection with the near-by land and has been the subject of discussion since Darwin, who was the first to try to explain the origin of the foundation on which the reefs have grown, as well as the peculiar ring shape of the atolls. He assumed the previous existence of a volcanic island with fringing reefs which submerged and left the ring shaped reef. Deep borings in recent time showed that this and other existing hypotheses explain the origin of only a small percentage of atolls. The « coral reef problem » still remains to be solved.

In the area of our investigations we had to deal with all kinds of reefs but without atolls. In the Indian Ocean the latter are confined to the Maledive Islands.

Along the coast of the continent reefs are rather poorly developed because of rivers that affect coral growth by producing low salinity and mud which covers suitable substrates. The offshore islands within the Malacca Straits, however, have well developed fringing reefs. The West-coasts of the islands off Sumatra (Nias Mentawai) are too exposed to the force of the trade winds and drop too fast to great depths to allow growth of coral belts of any importance and for the same reasons we were unable to anchor and work there. However, the coasts facing Sumatra have flourishing fringing, barrier and small platform reefs, sometimes connecting hole groups of islets, in one case even in the form of a ring, thus reminding one of an atoll.

Configuration. Existence or development of coral-reefs is possible wherever the ecological conditions are suitable. Their *shape* or *type* depend on geomorphic conditions and on hydrologic and meteorologic influences which are the cause for all kinds of variations and transitions. Therefore the coral associations of the various reef « types » are not significantly different, but provide comparable ecological conditions. Sections of near-land reefs may be compared with sections of atoll-reefs of which the configuration and zones are well defined. Rough-water reefs of fringing or barrier type which face heavy swells are comparable with atoll reef margins with algal ridges, calm-water reef correspond to reefs on the leeward-side of atolls, the calm-water zone between barrier-reef and land is perfectly comparable with lagoons and so on.

From the open sea towards the beach we may distinguish reef-slopes, algal ridges (if the reef is facing constant heavy swell), reef flats (possibly between two islands) and lagoons (between islands or between barrier reef and island).

The lowest zone on an exposed seaward slope (fig. 2) to which reefbuilding species extend is that of *Echinophyllia* (2). Toward

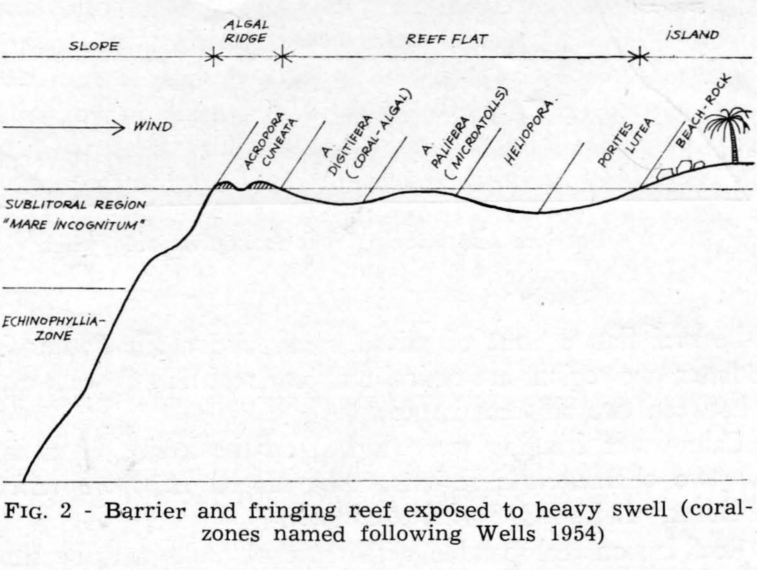

FIG. 2 - Barrier and fringing reef exposed to heavy swell (coral-zones named following Wells 1954)

(2) Since our own coral samples are not yet determined the dominant corals in the different zones will be named following Wells (1954). As far as we could see Wells results from Bikini can be generalized, sometimes perhaps only to genus level.

sealevel a sublittoral region follows with rich but, because of heavy breakers, not very well known coral population (« mare incognitum »). Then comes a reef margin with algal ridge (*Porolithon*) and *Acropora cuneata* followed by a barely submerged reef-flat with *A. digitifera* zone, *A. palifera* zone with microatolls consisting of *Favia, Favites, Platygyra, Goniastrea, Porites,* the zone of the blue octocorallian *Heliopora* and finally a *Porites lutea* zone next to the beach with dead coral rock.

At reefs facing variable winds (fig. 3) an algal ridge is wanting. On the slope we find a region of branching *Acropora formosa,* then,

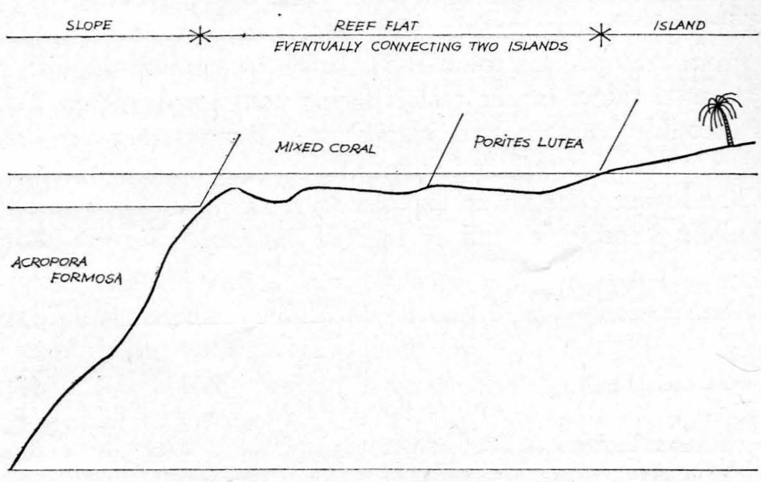

FIG. 3 - Barriere and fringing reef facing variable winds

on the reef flat, a zone of mixed corals and again *Porites lutea.* The latter two regions are typical for some reef flats as well, extending between two adjacent islands.

Calm-water fringing reefs (fig. 4) on the leeside of an island show two characteristic regions: table-shaped *Acropora reticulata* and clumsy digitiform *Porites Andrewsi.*

Reef lagoons comparable with those of atolls may be situated between barrier reef and island or between protecting islands (fig. 5). On the sand covered floor large growing Acropora (*A. reticulata* and *A. formosa*) and *Porites* flourish microatolls and small platform reefs are abundant.

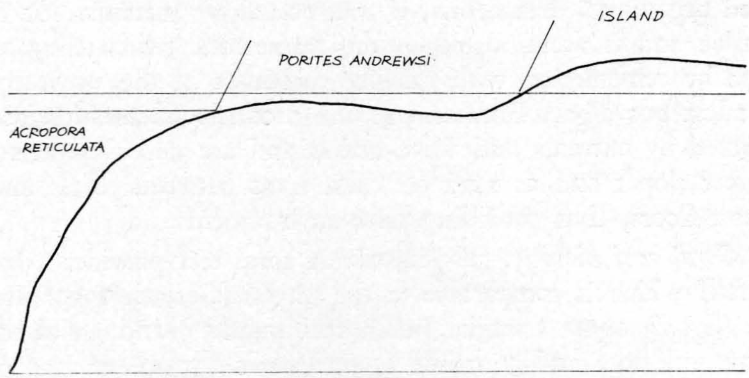

FIG. 4 - Calm-water fringing reef (lee of an island)

Construction and destruction. Construction and destruction of the reef is due to alternating biotic and abiotic functions and forces. A coral reef is principally a firm calcareous framework made by the skeleton of hermatypic coelenterates and calcareous algas. Its growth is therefore fundamentally a biological process. Geological processes (erosion and sedimentation) ensue, however, as soon as the first reef organisms are demaged by wave action.

Damage is made possible or at least speeded up by organic destruction by organisms such as dissolving algae, boring sponges, worms, barnacles, molluscs and echinoids and scraping fish (Scaridae, Monacanthidae). Erosion produces debris and sediments derived from organic and physical degradation of the frame and asso-

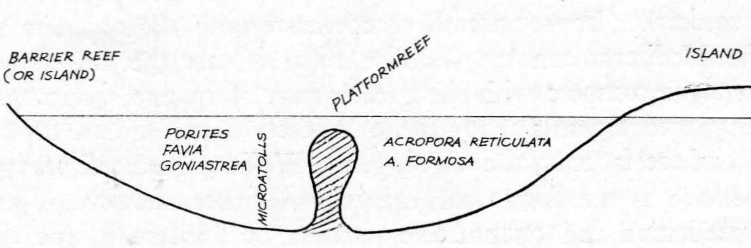

FIG. 5 - Lagoon

ciated organisms. The debris, if transported by currents, acts as an abrasive and is accumulated in the framework which they consolidate by cementation with calcium carbonate of the seawater and by calcareous algae. Furthermore the products of abrasion are distributed by currents and wave action and are deposited as rubble on reef slopes and as sand on calm spots between corals and on lagoon floors, thus providing new environments.

Coral reef biology. (a) general: A coral reef provides a habitat in itself which is comparable to the phytal (Gerlach 1959). It consists (fig. 6) of an essential (main reef builders) and an associated fauna and flora and a mobile fauna (Wells 1957).

To the essential fauna belong mainly hermatypic Coelenterates: Hydrozoa (*Millepora*) and Anthozoa (Octocorallia such as *Heliopora* and *Tubipora* and Madreporaria e. g. *Acropora, Porites*). An essential reperesentative of the flora is *Porolithon;* in some regions the algal genus *Halimeda* may become a dominating reef constituent.

These dominating organisms (alive, or their skeleton after death) provide substrate and ecological niche for epi- and endofauna and -flora, such as boring and microorganisms and other associated sedentary forms, such as plants, sponges, coelenterates, polychaetes, molluscs, tentaculates, tunicates and, for the reef dwelling mobile fauna, crustaceans, molluscs, echinoderms and fish.

(b) *ecology of sponges*: after this short characterisation of the reef habitat I would like to discuss some of the most important ecologic factors responsable for the distribution of a very abundant group of reef dwelling animals - the sponges. *Light*: since reef building corals are restricted to the euphotic zone light is a factor of considerable importance. My experience with the euphotic zone in the Mediterranean sea (Rützler 1963) is that the fast growing green algae compete with the greater part of sponge species which are displaced towards shady north exposed slopes and to caves. In the coral reefs only the algal genus *Halimeda* sometimes gains importance as the dominant organism. Also here however I found the qualitative and quantitative maxima of Porifera in the shady areas. This finding differs from the opinion of de Laubenfels who state (De Laubenfels 1950) that all tropical sponges (like corals) depend on the occurrence of holophytic symbionts in their tissue and are therefore photophilous. Besides the strong radiation energy in tropical shallow water there is also — because of the living coral — a lack of suitable substrates in the illuminated parts of the reef. The surface of dead solid substrate is very much exposed to sediments and to nibbling fish. Fishes of the following families have been observed feeding on sponges: Mullidae, Chaetodontidae,

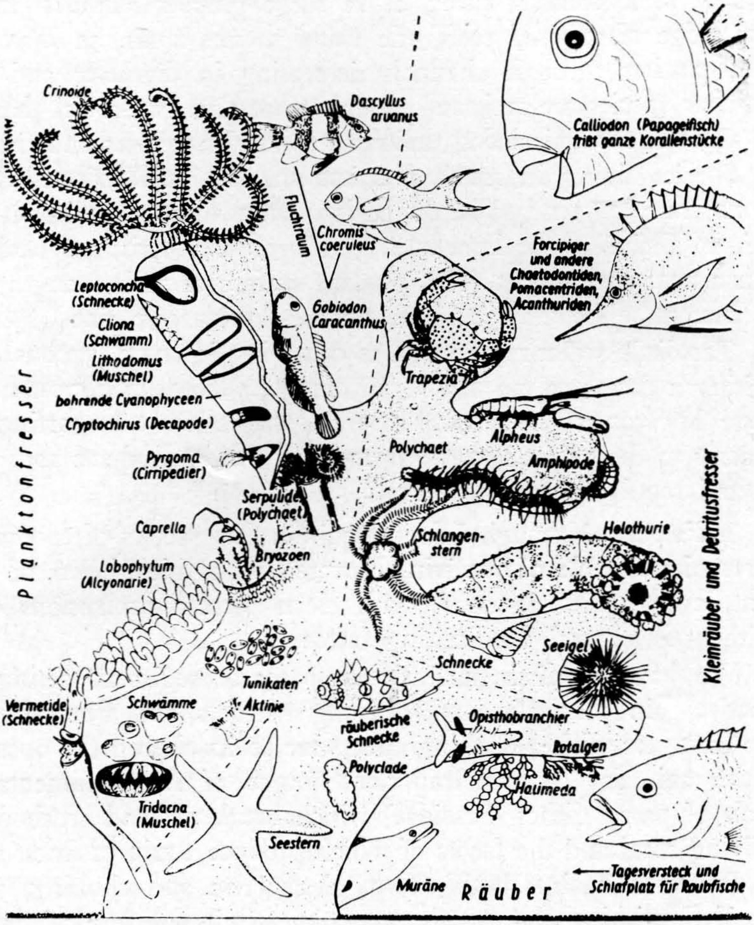

FIG. 6 - Reef habitat: essential, assoccited and mobile fauna (reproduced from Gerlach 1959)

Abudefdufidae, Labridae, Scaridae and Balistidae (Bakus 1963). Although there are some large and apparently fast growing sponges to be observed in fairly shallow, light exposed zones, the mentioned facts may be the reason or part of the reason, why most of the

Porifera are growing under dead coral rocks, in caves, on the lower side of tableshaped *Acropora reticulata* or on the dead base of the ramose wickerwork of other Acropora.

Water-movement: exposure to water-movement, currents or wave action can be limiting in both extremes. In the most narrow parts of some shallow caves, or in surge grooves common in the algal ridge of exposed reefs, the water masses attain an incredible speed passing through channels decreasing in diameter and only very few species are resistant enough to survive or protect themselves against mechanical destruction by living in crevices and fissures.

Species living in much less extreme but still agitated water are not rare but tend to be of the low encrusting type without projections. Flabellate or lamellate types are characteristic of habitats with a constant current. The inhalant surface of such sponges faces the current while the oscula are on the downstream side.

Too little water-movement, as occurring in some lagoons, is as limiting a factor as too much movement. For optimal growth moderate but constantly moving water is necessary, transporting nutriments to the animals, carrying away excretion products and detritus and regulating temperature.

Sediment: Although I found quite a few species of sponges in the tropics capable of surviving, covered with thick layers of sediment, even buried in sand, with clean oscular protrusions only, sediment is generally a limiting factor.

We have to distinguish between coarse sediment acting destructively in connection with strong currents and fine sediment in calm-water with a choking effect due to its closing the openings of the animals. A very important source of fine sediments are shoals of parrot fishes (Scaridae) which break off and crush pieces of living coral and the faeces of which produce a rain of finest sand.

Protected against both effects, destructive and choking, sponges, if flourishing close to the sea-floor, survive on vertical or, upside down, on horizontal substrates.

Substrates: as already mentioned light exposed surfaces in reefs consist mainly of living corals. They are able to clean themselves from sediment or prevent larvae from settling by producing slime in greater or lesser quantities. Still there are some few freeliving and, more frequently, boring sponges growing on or in living corals and I would like to learn which species are capable of doing so and how larvae protect themselves against destruction or against being carried away by slime.

Dead substrates if they are stable enough not to be turned over by waves show rich sponge populations on parts that are protected against sediment and other external effects already discussed.

Related habitats

Two distinct habitats can regularly be found in the neighbourhood of reef corals: sand, a product of the reef, and mangrove.

Sand: There are some sponges growing exclusively on sand in calm water, attached to some seaweed or small stone, others boring in stones covered by sand, protruding coniform papillae for the exchange of water. Others again are to be found actually buried in sand and mud, with sand-encrusted base and uncovered protrusions: *Biemna fortis* and *Anthosigmella vagabunda*. The latter species showed an interesting type of asexual reproduction resembling that of mangrove-trees: One of the oscular protrusions grows into a sphaerical « bud », the conical stalk becomes thinner until it breaks and the « bud » drops on the floor. It now sends a new « root » into the sand, thus anchoring and growing into a new sponge.

Mangrove: Sites favourable to mangrove trees (*Rhizophora, Avicennia*) are swampy seacoasts with rich sediment of loose mud. They are mostly found where islands provide a lee, in estuaries and lagoons. The geographical distribution of the mangroves roughly covers that of reef corals although it extends generally slightly further North and South and also flourishes on the central-West-sides of Africa and America.

The plants are euryhaline, even capable of surviving in fresh water; their branches and characteristically long roots provide substrate and hiding place for land, semiaquatic and marine animals (fig. 7).

The mangrove floor and adjacent flats consist of mud made foul by dead organisms. Carbonic acid produced by decomposition of organic matter and tannic acid from the mangrove bark cause rapid corrosion of calcium carbonate. This is demonstrated by the etched shells of the snail genus *Pyrazus* (Revelle & Fairbridge 1957).

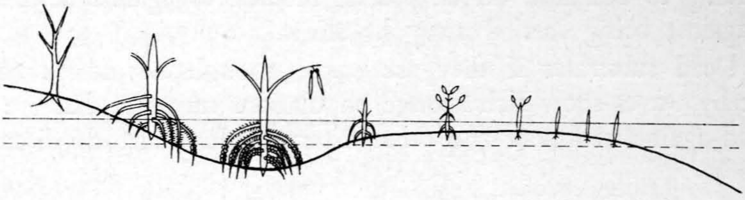

FIG. 7 - Mangrove with adjacent flat (exposed at low tide)

There are two types of mangrove-dwelling sponges: those growing on perpetually submerged parts of the roots and those buried in mud and sand. The latter, such as *Biemma fortis* and *Anthosigmella vagabunda* mentioned above are able to survive exposure to air at low tide when the flat becomes uncovered. Because of the limited space on mangrove-roots and the steady production of new substrate this area is ideal for observation of succession and competition.

SUMMARY

With this brief survey I hope to have shown the complexity in the biological structure of a coral reef. Since many authors within the last hundred years have been fascinated by the reef habitat we know many geological, physiological and ecological details. One of the major problems, the origin of atolls, is still only partially solved.

We have learned about the general zonation of reefs, indicated by the main constituents of reef building organisms. In contrast to the rocky littoral of Northern seas coral reefs are *living* units providing highly specialized ecological conditions for their inhabiting fauna and flora.

The phylum Porifera has been selected for discussing some of the most important ecological factors affecting reef organisms such as light, water movement, sediment and substrate.

Habitats to be found regularly in the neighbourhood of coral reefs are sand and mangrove. Although sand is little suited to the existence of sedentary organisms there are some few sponges adapted to this special environment.

Mangrove swamps provide an extraordinary habitat favourable to several species of Porifera flourishing on the roots of the trees.

Research in tropical littoral waters, especially in the upper region within the range of coral reefs, is a very young branch of the biological science. Since skin and aqualung diving is no longer a method reserved for sportsmen many methodical difficulties in collecting and investigating have been mastered. Our TE VEGA Expedition proved again the value of this method combined with a well equipped floating laboratory.

Realizing the tremendous amount of money beeing spent for physical oceanography and deepsee research one wishes there were more floating laboratories adapted for coastal research contributing to our knowledge of the littoral region, one of the most heterogeneous and fascinating territories in the sea.

RIASSUNTO

Con questa breve rassegna spero di aver mostrato la complessità della struttura biologica di una barriera corallina. Poichè molti AA. negli ultimi cento anni sono stati affascinati dall'habitat della scogliera noi conosciamo molti dettagli geologici, fisiologici ed ecologici.

Uno dei maggiori problemi però, l'origine degli atolli, è ancora solo parzialmente risolto.

Ho discusso la zonazione generale delle scogliere indicandone i principali costituenti fra gli organismi costruttori. In contrasto con il litorale roccioso dei mari settentrionali le scogliere coralline sono unità viventi provviste di condizioni ecologiche estremamente specializzate per la fauna e la flora che le abitano.

Il phylum Porifera è stato scelto per discutere alcuni dei più importanti fattori ecologici che influenzano gli organismi della scogliera quali luce, movimento delle acque, sedimento e substrato.

Gli habitat che si trovano normalmente in prossimità delle scogliere coralline sono sabbiosi e a mangrovie. Sebbene la sabbia è poco adatta per la esistenza di organismi sedentari vi sono alcune poche spugne adattate a questo speciale ambiente.

Le paludi a mangrovie costituiscono un habitat straordinario favorevole a numerose specie di Poriferi che si sviluppano sulle radici degli alberi.

La ricerca nelle acque tropicali litorali, specialmente nella regione superiore entro l'estensione della barriera corallina, è un ramo molto giovane della biologia. Da quando il sommozzamento mediante autorespiratori non è più un metodo riservato agli sportivi, molte difficoltà nei metodi di raccolte e d'investigazione sono state dominate.

La spedizione Te Vega ha provato di nuovo il valore di questo metodo combinato con un laboratorio galleggiante bene attrezzato. Considerando la enorme quantità di denaro che è stata spesa per l'oceanografia fisica e la ricerca di mare profondo si vorrebbe che ci fosse un maggior numero di laboratori galleggianti adattati per la ricerca sulle coste e che contribuiscano alla nostra conoscenza della regione litorale, uno dei più eterogenei e interessanti territori nel mare.

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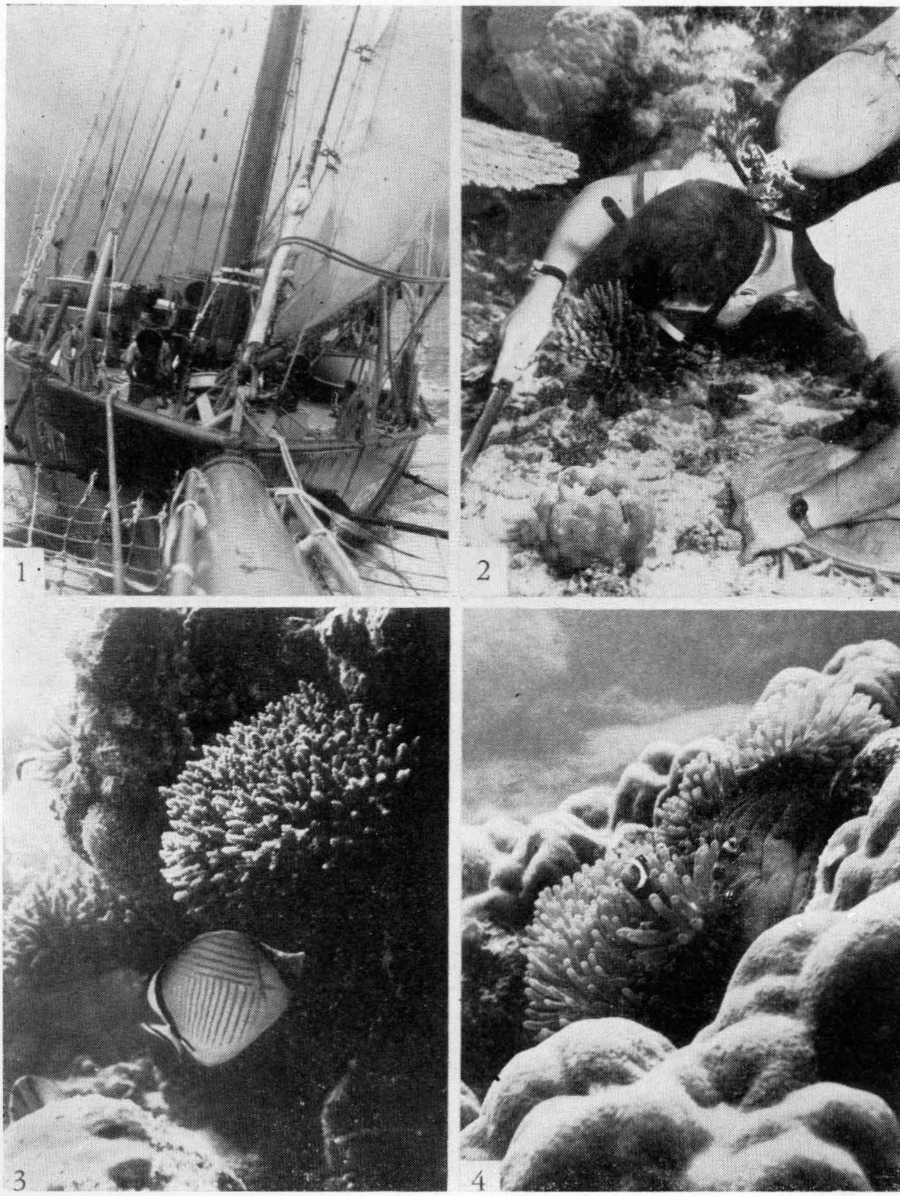

TAV. I

1 - The Research Schooner TE VEGA sailing across the Andaman Sea.

2 - Aqualung equiped student collecting corals on lagoon floor.

3 - A common buterfly fish (*Chaetodon vagabundus*) searching for food on read coral base. These fishes were also observed feeding on sponges.

4 - Anemone (*Stoichactis*) with hiding « clown » fish (*Amphiprion*) is a common associated reef organism.