

Deep-water exploration of the Red Sea by submersible

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Abstract: The steep continental slope of the Red Sea beyond the euphotic zone contains the least known biota of the Red Sea. More knowledge exists on the Red Sea's deep sea than on this transitional zone between photic and aphotic depth. Since 1981, with the help of the research submersibles "Geo" and "Jago", over 430 dives to a maximum depth of 402 m were carried out at various locations off Djibouti, Sudan, Egypt, and Israel; the topics covered include biology, microbiology, physiology, geology, geophysics, and oceanography. The submersible exploration of the Red Sea's twilight zone is a new, modern step continuing the classical surface-bound deep-sea expeditions which started in the 19th century - of which the Austro-Hungarian "Pola" expeditions were among the first.

Introduction

The intermediate depth or twilight zone between the light-flooded, productive shallow waters and the cold, lightless deep sea contains the least known biota of the world's oceans. Probably more knowledge exists on the deep sea than on those transitional zones between photic and aphotic depths. Here, between 100-400 m, light progressively fades out and photosynthesis, the motor of primary production, rapidly loses its direct impact on the production of organic carbon. Only 5 % of the photosynthetically produced carbon reaches depths below 200 m through remineralization (JANNASCH 1986, 1987). All these factors have a paramount influence on feeding and feeding types of organisms, and gradients in light and nutrients are immediate structuring forces of communities in this light- and nutrient-limited realm. Therefore, the intermediate depth range of the world's oceans is, compared to shallow seas and the deep sea, an equally important research field, even though our knowledge on this part of the ocean is rather poor.

The Red Sea, since the Pliocene an ocean in the making, with its unusual topography and evolutionary history and its uncommonly high water temperature of 21.7 °C down to 3000 m depth, is defined as a secondary sea (KLAUSEWITZ 1989). Surrounded by deserts and separated from the Indian Ocean by the shallow sill of the Bab El Mandeb, the isolated Red Sea trench and the adjacent deep basin of the Gulf of Aqaba led to evolutionary divergences in many animal phyla (KLAUSEWITZ 1989, POR 1975, 1978). The high rate of endemism, particularly among littoral fishes, is well studied (KLAUSE-

WITZ 1983, 1989, GOREN 1986, ORMOND and EDWARDS 1987). During the Pleistocene the different glacial periods led to changes in water temperature, salinity, and sea level. This had drastic effects on the Red Sea's ecology (BRAITHWAITE 1987, SHEPPARD et al. 1992). Periods of severe climatic conditions with high salinity and low surface temperatures were followed by periods with subtropical and tropical conditions. At the end of the last glacial (Würm) about 11 000 years ago, the present subtropical-tropical status was established. The eustatic lowering of the sea level during glacial maxima and the subsequent rising of the sea level during warm periods left coastal landmarks behind - a kind of geological signal - visible today as terraces of biogenic origin. High water marks are located in shallow water or on land, while the water marks of cold glacial periods are mostly hidden in deeper waters (SHEPPARD et al. 1992, GVIRTZMAN et al. 1977, REISS and HOTTINGER 1984).

In 1981, our submersible research group started deep diving operations with the submersible "Geo" down to 200 m depth off the coast of Egypt, Israel, Sudan, and Djibouti. Since 1989, the submersible "Jago" is available with a greater depth capacity of 400 m (Fig. 1). The submersible was named after a small deep-sea shark of the Red Sea, *Iago omanensis* (BARANES and BEN TUVIA 1979).



Fig. 1: Two-man-submersible "Jago" with depth capacity of 400 m. The weight of the craft is 3.3 tons.

Scientists of various disciplines joined our operations and over the years a total of 430 dives increased our knowledge of the Red Sea's intermediate depths. The present paper provides a brief overview of the different tasks and

observations carried out by our team. The arbitrary selection made here emphasizes topics relevant to the formation of submarine landscapes, thus linking geological events and biological processes.

Submarine structures, ancient sea level, and coral growth

Submarine terraces

For historical reasons I begin with our exploration of drowned Pleistocene terraces and the depth limits of coral growth. At various locations along the coast of the Gulf of Aqaba and the Red Sea proper, echosounding profiles revealed - depending on slope angle - massive sand-covered platforms, boulders, or protruding edges at 40, 60, 80, 90, 105 and 115-120 m depth (Fig. 2). A further structure was sometimes detectable at 180 m, but could not be verified at all sites. Because the depth strata of the different structures were identical along the coastline, it was evident that different glacial events were responsible for the geological formations. We found a "curriculum vitae" of different glacial events, i.e., maxima of cold periods with low stands of the sea level. The counterparts of warm periods, with high water marks, are known from various parts of the world (WERTH 1953, and others). To our surprise, identical depth marks at various sites indicated that differential tectonic movements of the Red Sea trench after the formation of the terraces did not alter the depth range of the former sea level marks.

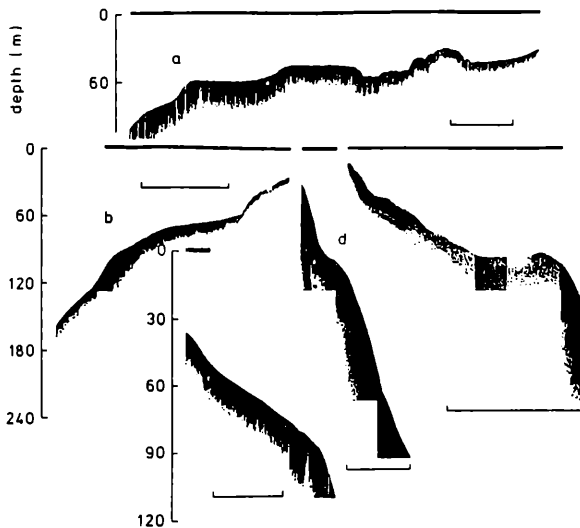
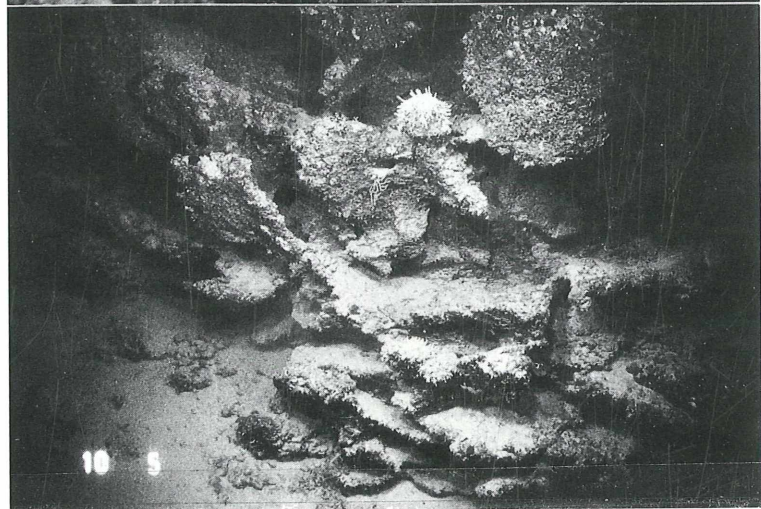
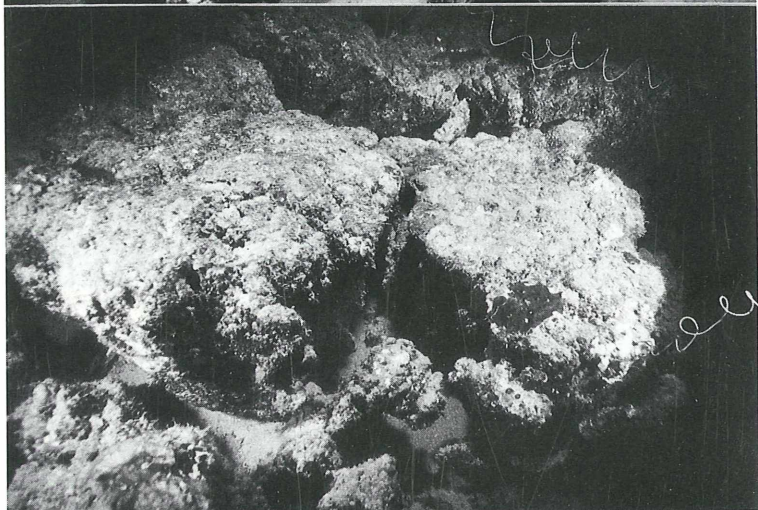
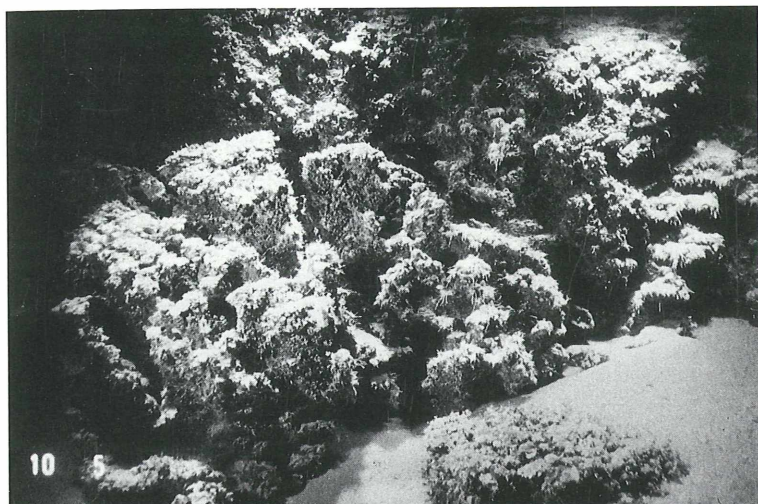


Fig. 2: Echoprofiles taken perpendicular to the coastline along different locations off the Sinai coast, Egypt. (a) Ras Burka, course 100 degrees, (b) Fjord, 140 degrees, (c) Faraun Islands, 290 degrees, (d) Ras Um Sid, 320 degrees, (e) Wadi Hadmiya, 265 degrees.

Our task was to identify the framebuilders of the ancient carbonate reef structures. Their identification was difficult because they were heavily overgrown by recent biogenic crusts of varying thickness. However, some locations revealed reef-building corals with growth forms typical for the ecophenotype of shallow water (Fig. 3). Aging the terraces turned out to be extremely difficult due to contamination of the rock samples by recent growth of calcareous organisms.

In the last two decades two competing hypotheses of the Red Sea's past have been discussed. GVIRTZMAN and colleagues refer to the Red Sea as a hypersaline environment, while YUSUF (1976) and BRAIHWAITE (1987) favour the "Great Evaporation" hypothesis, with the Red Sea being disconnected from the Indian Ocean by the shallow sill of the Bab El Mandeb. Our direct observations of the submarine terraces and limited rock sampling established biogenic framebuilders and the corallogenic origin of the fossil terraces, at least in our observed depth range. More selected sampling in deeper zones of the rock must be done in order to more precisely follow the time scale of the glacial events and the morphogenesis of the Red Sea's submarine terraces. The terraces are perfect indicators for ancient sea level changes and therefore of particular interest for geology, paleoecology, and climatology, not only for the Red Sea.

Fig. 3: Sunken Pleistocene terraces with growth forms of probably fossil corals. Top: lobate form, 105 m, Middle: globose form, 92 m, Bottom: foliaceous form, 105 m.



Submarine canyons

The Red Sea is surrounded by hot and arid deserts. Nevertheless, particularly during winter, occasional catastrophic flash floods discharge through wadis and transport terrigenous sediments into the sea (Fig. 4). Sediment-loaded gravity currents cut their way through the Pleistocene terraces and form deep canyons (BEN AVRAHAM et al. 1979).

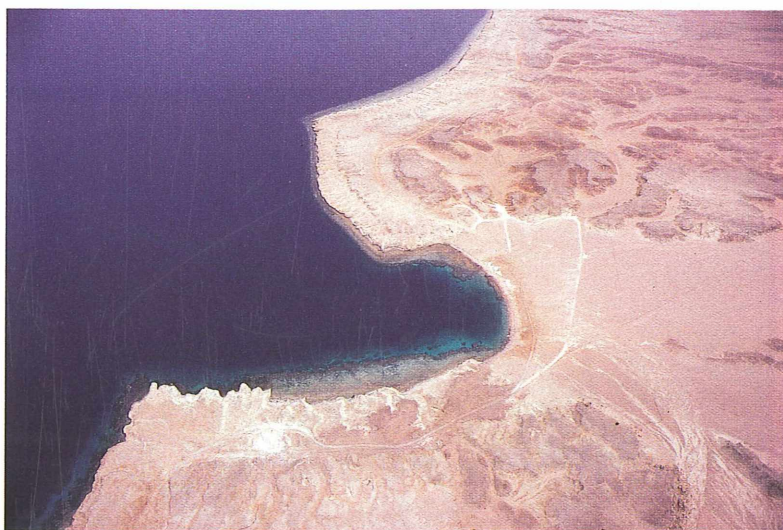


Fig. 4: Aerial view of the mouth of dry river beds along the Sinai coast, Egypt. Top: wide estuary with large amount of transported sediments in the Northern Sinai, Bottom: mouth of Wadi Hadmiya, Southern Sinai, with entrance in submarine canyon.

Earlier Red Sea canyons reaching down to depths of 130 m were thought by GVIRTZMAN and BUCHBINDER (1978) to have been formed by intensive subaerial erosion during Würm glaciation and drowning during the Holocene sea level rise. To test this hypothesis we studied the canyon off Wadi Hadmiya, Egypt, in more detail (FRICKE and LANDMANN 1983) (Fig. 5). Erosional scars - traces of gravity currents - were visible along the trajectories of the canyon (Fig. 6). Coral growth on top of these scars made date estimations of the last catastrophic gravity current possible and confirmed a time interval of approx. a decade. A flow rim along the deepest part of the canyon, partially filled with debris of shallow-water or terrigenous origin, indicated long-distance transport (Fig. 6); downwellings were also detectable. The filterfans of corals growing in the canyon bed were positioned perpendicular to the canyon direction and were good indicators for the major current flow (Fig. 7).

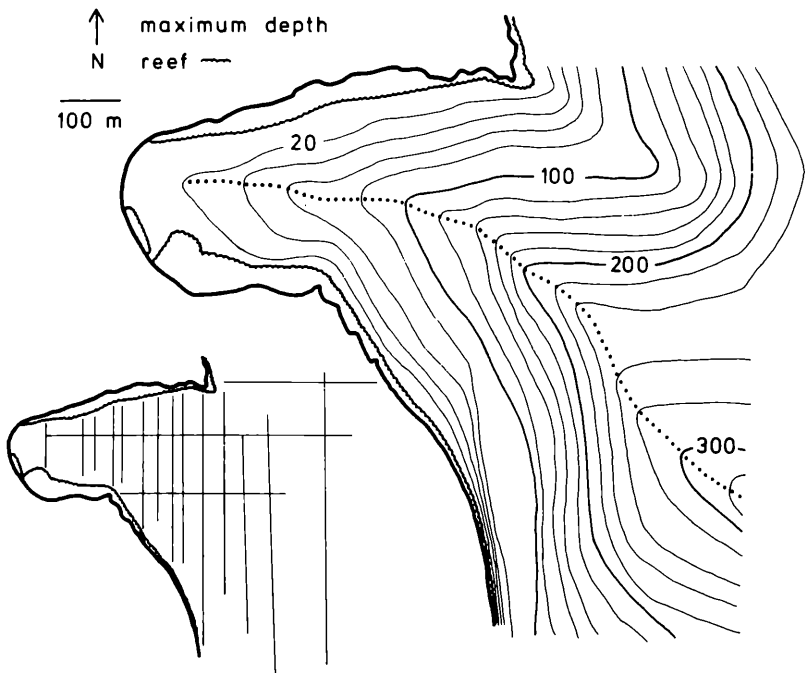


Fig. 5: Bathymetry of the submarine canyon in front of Wadi Hadmiya, Egypt. Track chart (lower left) shows echoprofiles which were used to construct the larger contour map.

The Red Sea canyons - miniatures compared with the huge canyons off the Nile, Ganges, or Hudson River - provide not only the deep-sea organisms with debris and particulate organic matter, but may also function as an important flow channel for downward transport of dissolved organic matter. At least in the Red Sea, this is apparently more important for the nutrient supply of

benthic communities in deeper waters than previously anticipated. This topic requires further research.

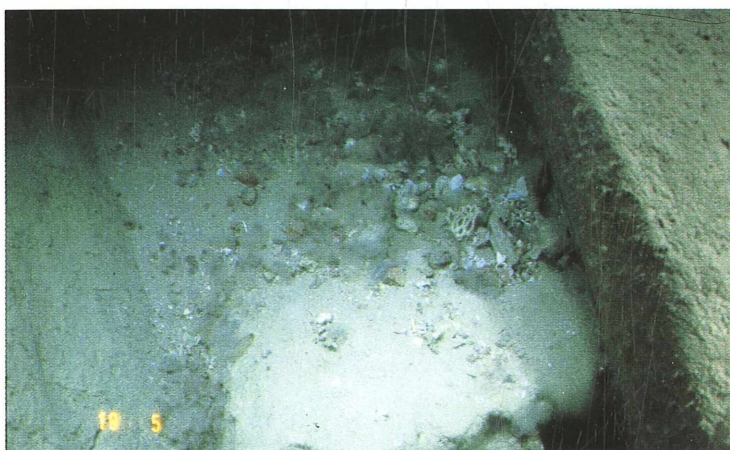
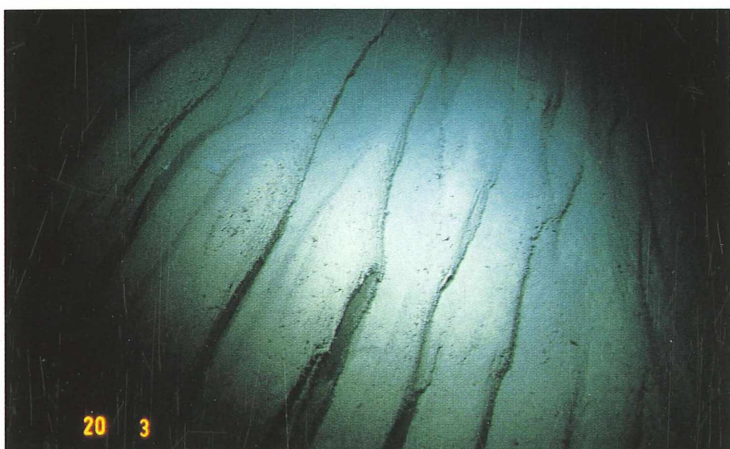
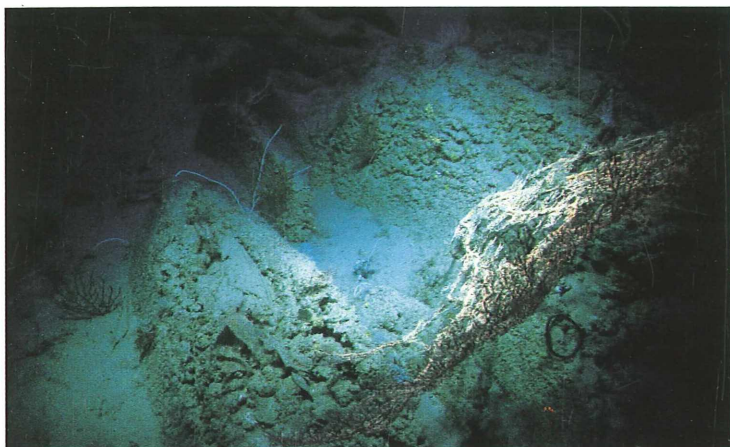
Our submersible observations confirmed that the canyons cut their way through all existing Pleistocene terraces. It is reasonable to assume that their formation is indeed an ongoing process sustained by recent gravity flows, common in all oceans of the world. The subaerial erosion-hypothesis for Red Sea canyons and a subsequent sea level rise during the Holocene is therefore highly unlikely.

Laminar micrite crusts

In 1981 we found a peculiar type of slow-growing hard bottom structure along steep walls below approx. 170 m (FRICKE 1982). Shingle-like structures, covered on top with sediments, grew on the surface of steep rocky walls (Fig. 7). A variety of sciaphilic calcareous organisms grew beneath the shingles, mainly serpulids, bryozoans, and asymbiotic corals. The interactions of sedimentation on top (preventing biogenic growth) and accretion on the underside and along the edges of the shingles seem to be the structuring forces of the formation. Recently, DULLO et al. (1990) and BRACHERT and DULLO (1990, 1991) described in more detail the shingle structures as laminar micrite crusts, and by radiocarbon dating determined growth rates of 3.5-10 mm/1000 a. They concluded that the crusts occur below the lower limit of coralline algae growth (approx. 120 m) and in waters deeper than the maximum drop of the Pleistocene sea level, i.e., the formation is due to biogenic processes unrelated to the photic zone. We can expect similar structures in aphotic depths exposed to high sedimentation.

Fig. 6: Traces of gravity flows in the submarine canyon of Wadi Hadmiya. Top: 115 m, overgrown eroded ridges with recent coral growth. Note the orientation of the coral fans as indicators for the major current flow within the canyon. Middle: 203 m, scoured erosional traces of gravity flows 5-7 m above the canyon floor, Bottom: 195 m, flow channel along the base of the canyon with remains of materials of shallow-water origin.

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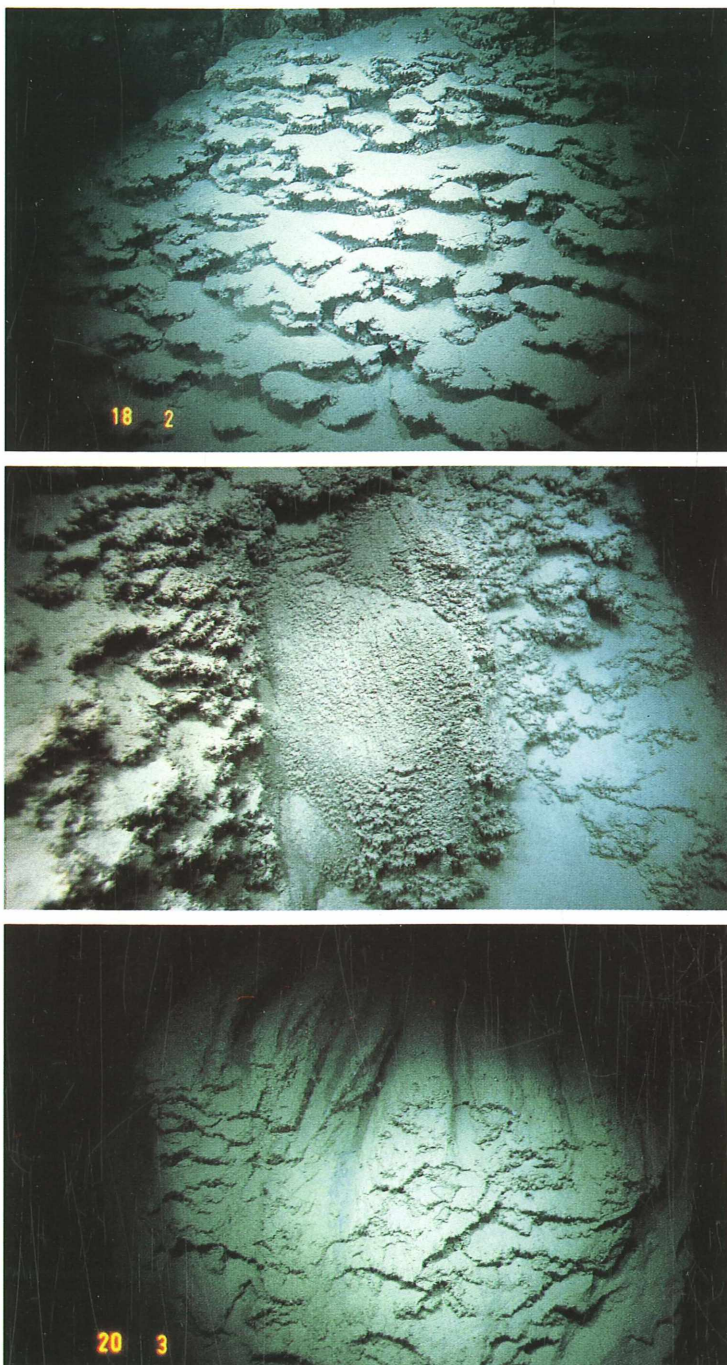


Fig. 7: Formation of laminar micrite crusts. Top: shingle-like structures along a steep wall, 182 m depth. Middle: micrite crusts along the walls of a small sedimentary cone, 180 m. Bottom: micrite crusts in a current shadow below erosional scars of gravity flows, 203 m.

Bioherms of asymbiotic corals

Another unexpected reef-like structure was built on rocky outcrops by the stony coral *Madracis interjecta*. The skeletons of the asymbiotic coral were framebuilders and were overgrown by a diverse benthic community (FRICKE and HOTTINGER 1983) (Fig. 8). Such bioherms of asymbiotic corals have been reported from other oceans and described as coral banks, coral structures, coral architecture or mounds (summary in FRICKE and HOTTINGER 1983). The *Madracis* coral does not harbor endosymbiotic algae. The absence of these algae below the euphotic zone does not hamper the formation of bioherms by stony corals. The *Madracis* bioherms are true reefs in the definition of the term in the Earth Sciences; they are surrounded by selected detritic facies types similar to ordinary sheltered patch-reefs in the shallow photic zone.

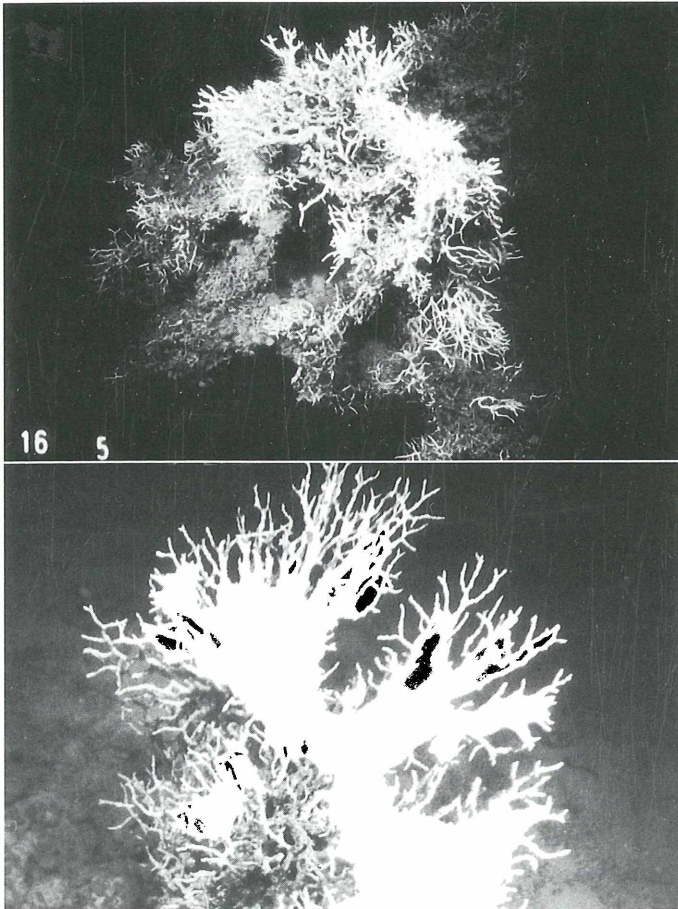


Fig. 8: *Madracis interjecta*-bioherm. Top: monotypic bioherm of *M. interjecta*, 165 m, Bottom: in-situ, the tree-like *M. interjecta* appears whitish but immediately turns red when exposed to air.

Deep-water symbiotic corals

A submersible is a very suitable tool to investigate the growth limits of contemporary coral reefs. In the Gulf of Aqaba we studied in great detail the depth limits of most reef-building symbiotic corals and investigated the influence of decreasing light on growth forms (FRICKE and SCHUHMACHER 1983). Due to limitations of photosynthesis and calcification, all symbiotic corals undergo a dramatic change in growth form with depth: they become successively flatter in shape (Fig. 9). Massive coral growth terminated at around 60-80 m depth, although coral outcrops of flat forms occurred down to 100 m. We found 9 symbiotic species at 100 m; one coral, *Leptoseris fragilis*, extended even down to 145 m, i.e., far below the 1 % light level, the limits of the euphotic zone.

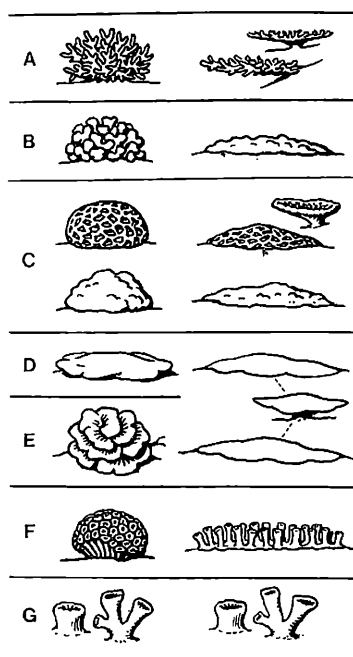


Fig. 9: Depth-dependent growth form of different corals, left: shallow water, right: deep water. A - branched treelike and bushy form, B - lobate or club-shaped form, C - globose to hemispherical form, D - explanate form with foliaceous, upfolded edges, E - foliaceous form, F - phaceloid form, G - solitary form.

Stony coral communities between 100-200 m depth

We applied, for the first time from aboard a submersible, line-transect methods to measure the diversity, density, and coverage of stony coral communities between 100-200 m (FRICKE and KNAUER 1986) (Fig. 10).

Along our transects we found a total of 11 species arranged in three distinct zonations, with a symbiotic coral, namely *L. fragilis*, being the most dominant form between 100-130 m. It is surprising that in a light-limited environment the only photosynthesizing coral outnumbers all remaining coral representatives. The benefits of photosynthesis are probably the main selective agent for the ecological success of the coral *L. fragilis*, which forms deep-water reefs, and dating revealed an age of several thousand years.

To the limits of marine photosynthesis

The Red Sea is a remarkably clear water body. On "Geo" dive 209 we could clearly identify the surface wave action from a depth of 135 m, a value only exceeded by the clear water of the Sargasso Sea, with 183 m vertical visibility ("Jago" dive 245). The limits of the Red Sea's euphotic zone are located at about 90-100 m (Fig. 11), a value not uncommon for tropical seas. The search for benthic photosynthesizing organisms inhabiting a progressively light-limited environment of a very narrow spectral window and the study of their specialized light-absorbing structures is an appealing task. We can provide the following observations.

At the Sinai peninsula, Egypt, we encountered dense colonies of the "upside down" jellyfish *Cassiopeia* sp. at 95-105 m (Fig. 12). They were greenish in appearance and contained dense aggregations of the endosymbiotic algae *Symbodinium* sp. This medusa is usually a specialized, shallow-water dweller of lagoons, living here under conditions of superabundant light. We have no explanation why *Cassiopeia* also occupies such extreme deep-water habitats, where benefits from the alga's photosynthesis are probably minute. The same also holds true for the endolithic algae *Ostreobium* sp., which penetrates the skeleton of living corals, also giving its host a greenish appearance. We found the filamentous green algae not only in almost all specimens of the symbiotic coral *Leptoseris fragilis*, but in many other corals at that depth. The algae occur down to a maximum depth of 190 m. In situ we were unable to measure with our means the alga's oxygen evolution because of extremely low production rates (Fig. 13). The algae infest almost all living corals at that depth, indicating that some benefits may recruit from the close vicinity of the living coral tissue, which is often only microns away. One could speculate that the algae take advantage of the coral's metabolic wastes, thus enabling them to penetrate the extreme depth. It needs to be established if the interaction is indeed a mutualistic, a commensalistic, or even a parasitic one.

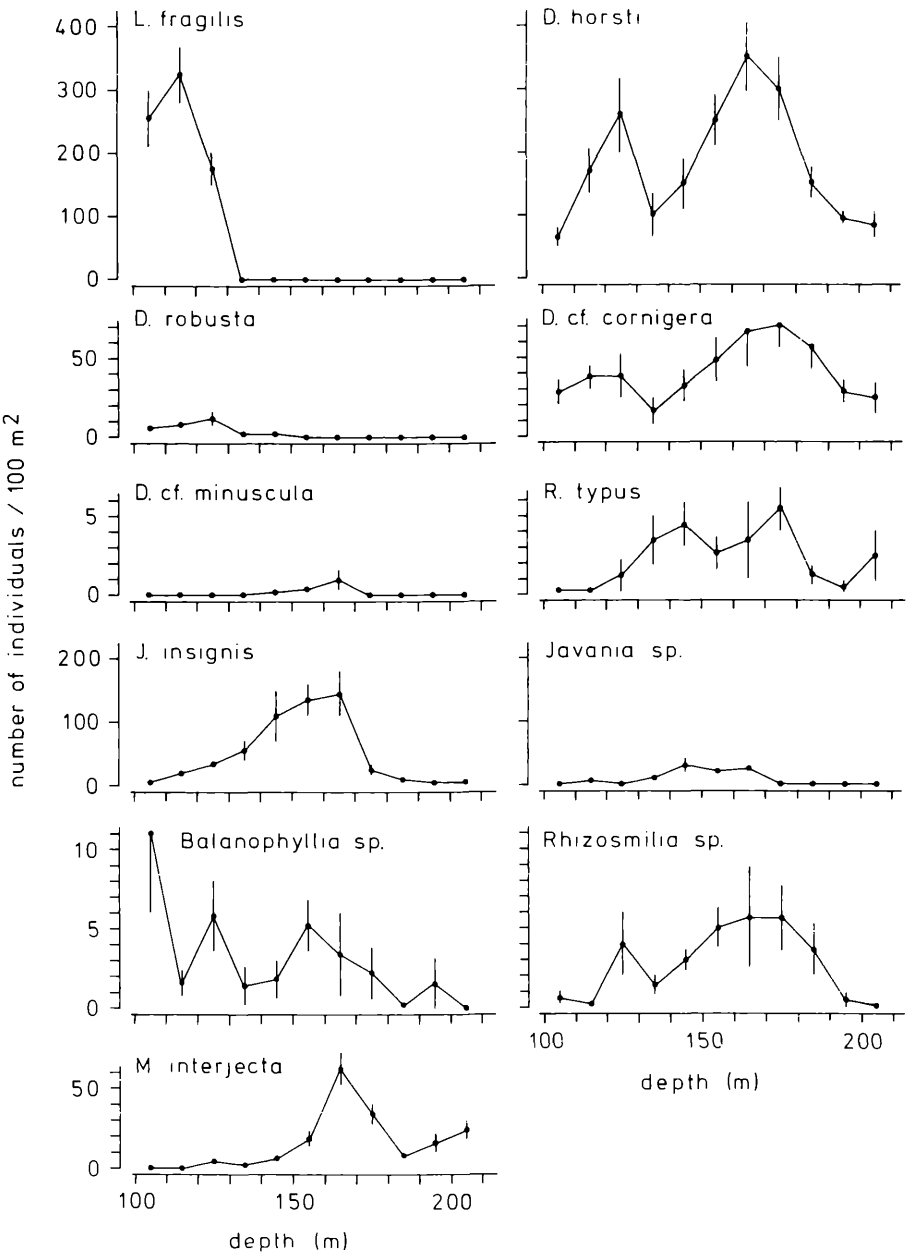


Fig. 10: Population density of stony corals between 100-200 m depth in the northern Gulf of Aqaba measured along 11 transects. The sampling unit has a size of 5 m². The data are pooled in 10 m-depth classes and presented as numbers of individuals on 100 m² with means and SD (n = 13-130 observations per depth class).

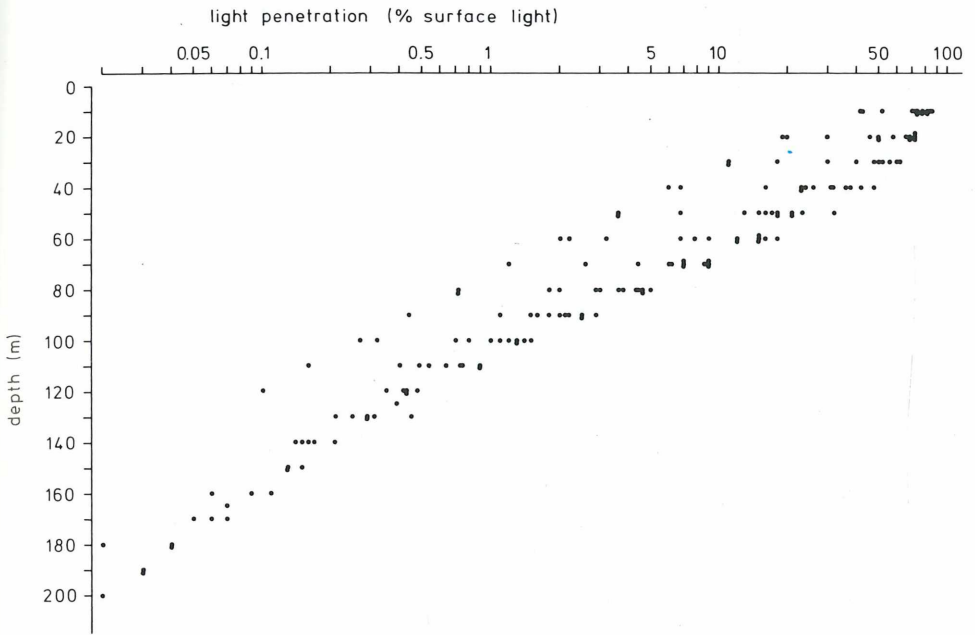


Fig. 11: Depth profiles of cumulative light penetration in the Red Sea at noon on cloudless days taken during different seasons of the year. Light penetration was measured with a Licor Quantum Radiometer LI 188 B and LI 195.

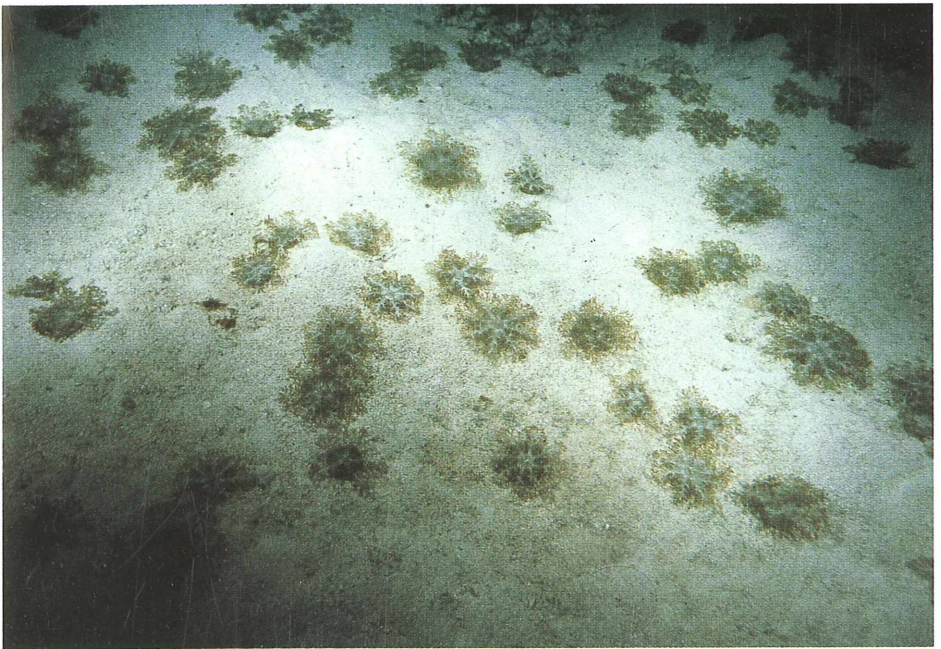


Fig. 12: The benthic medusa *Cassiopeia* sp. at 95 m depth, Sharm El Sheik, Egypt.

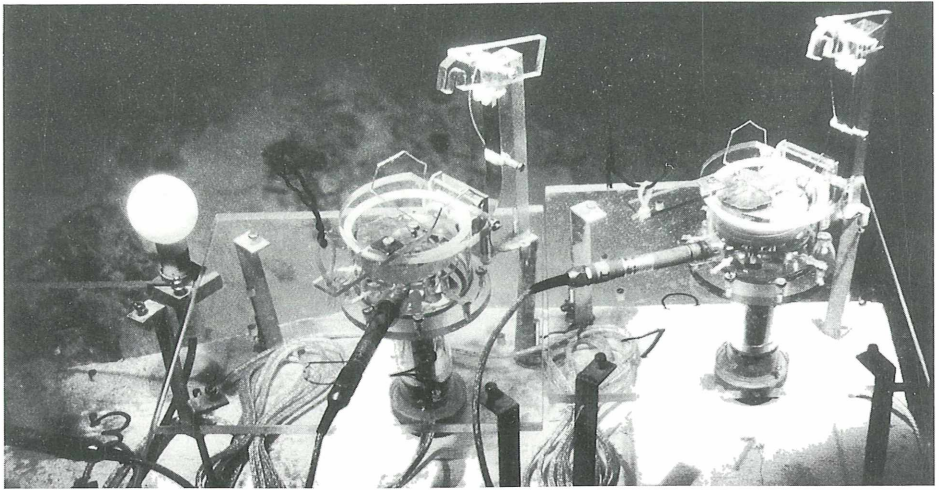
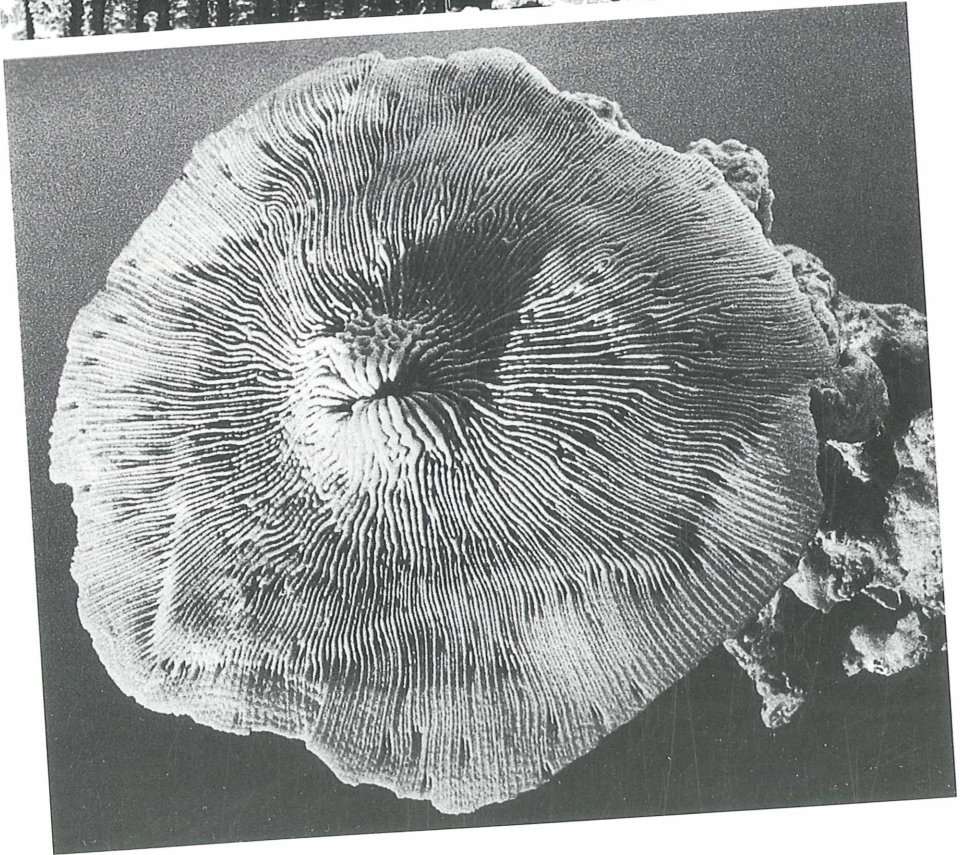
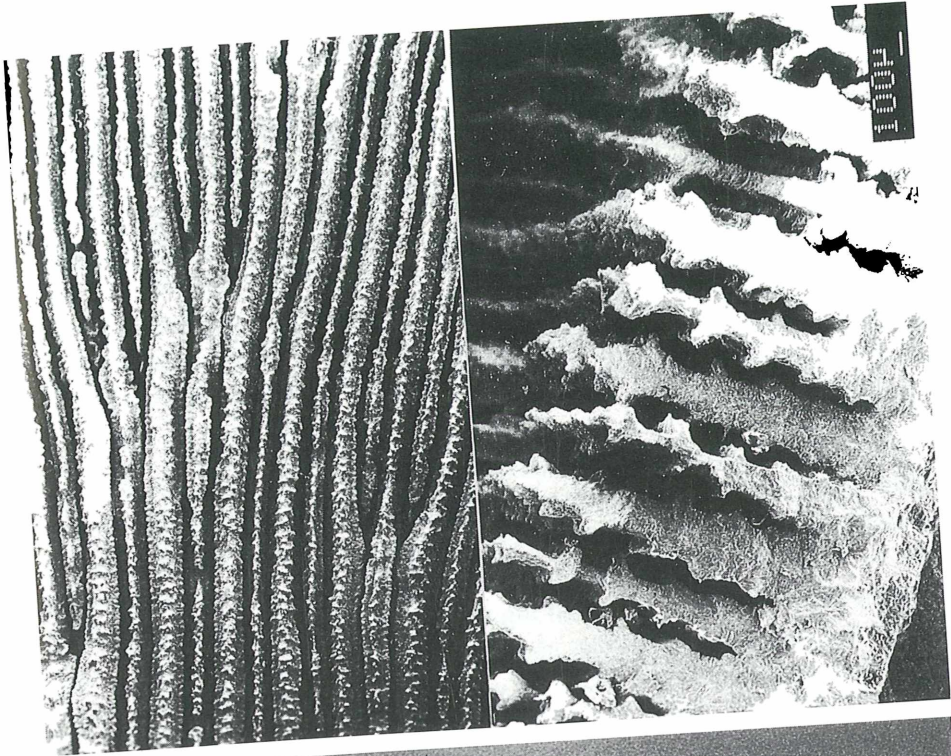


Fig. 13: In-situ measurements of oxygen evolution with respiration chambers mounted in front of the submersible "Geo".

How a photosynthesizing organism can cope with the extreme low light intensities of a narrow spectral composition at intermediate depth was studied in the coral *L. fragilis* (SCHLICHTER et al. 1986, FRICKE et al. 1987, SCHLICHTER and FRICKE 1988) (Fig. 14). For the human eye, this coral appears almost black in situ, i.e., all incoming light is fully absorbed. The morphology and photoecology of *L. fragilis* revealed some surprising coevolutionary traits between the coral host and the algal symbiont. The coral surface, with its calcareous septae, shows a very peculiar slipper-like structure (Fig. 14) - a complicated transport system (FRICKE and KNAUER 1986) and an ideal light trap.

Fig. 14: The symbiotic coral *Leptoseris fragilis* with dorsal view (top left) and scanning micrographs showing the arrangements of the calcareous septae (top right) and tree-like structure in cross section (bottom right).

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From onboard the submersible we measured the production rates (Fig. 15 top) and calcification with radioactive tracers. We found a compensation depth where production rates slowly exceed the respirational demands of the coral-algal complex - at levels of approx. 100 m or, in photon flux units, $1.0 \mu\text{Em}^{-2} \text{ sec}^{-1}$. No other known symbiotic coral has this capacity (Fig. 15 bottom). *L. fragilis* has an extremely low growth rate. Marked corals at 90-120 m depth showed growth increments of mean 0.6 mm per year ($\text{SD}=0.1 \text{ mm}$; $n=47$). From onboard the submersible, the individual history of marked corals was followed by photographic means over several years. There were no dramatic changes in size class distribution, indicating stable and slow-growing populations.

The ultrastructure of the coral tissue revealed a hitherto unknown pigment shield (SCHLICHTER et al. 1986), whose function we examined. The spectral composition at this depth contains considerable amounts of long ultraviolet light of 380-400 nm. But long ultraviolet light can hardly be absorbed by ordinary chlorophylls of the host algae. The host coral therefore evolved a specialized pigment system that absorbs long UV and shifts the short wavelengths by autofluorescence in longer wavelengths suitable for photosynthesis (SCHLICHTER et al. 1986, SCHLICHTER and FRICKE 1991). When the coral is excited with long ultraviolet light of 380-390 nm, it emits light of 460-470 nm by fluorescence the maximum absorption peak of the symbiont's chlorophyll is located here (Fig. 17). The host coral harvests light in favour of its photosynthesizing symbiotic algae. The few photons penetrating the water column are caught by specialized morphological structures and pigment systems of the host, thus exploiting and harvesting light of all available wavelengths. The pigment system of corals collected at 120 m was destroyed after a one-year exposure in light fields of shallower depth (Fig. 17).

This raises the question of how, by coevolution, natural selection was able to select for such complicated interlocking processes and morphological functions between different organisms. We still cannot appreciate the benefits for the host coral. The evolutionary costs of the many biochemical pathways and morphological structures - as seen through the eyes of a human observer - seem to exceed the minimal net-income for the carbon budget of the coral host. Perhaps there are other benefits recruiting from some essential photo-assimilates.

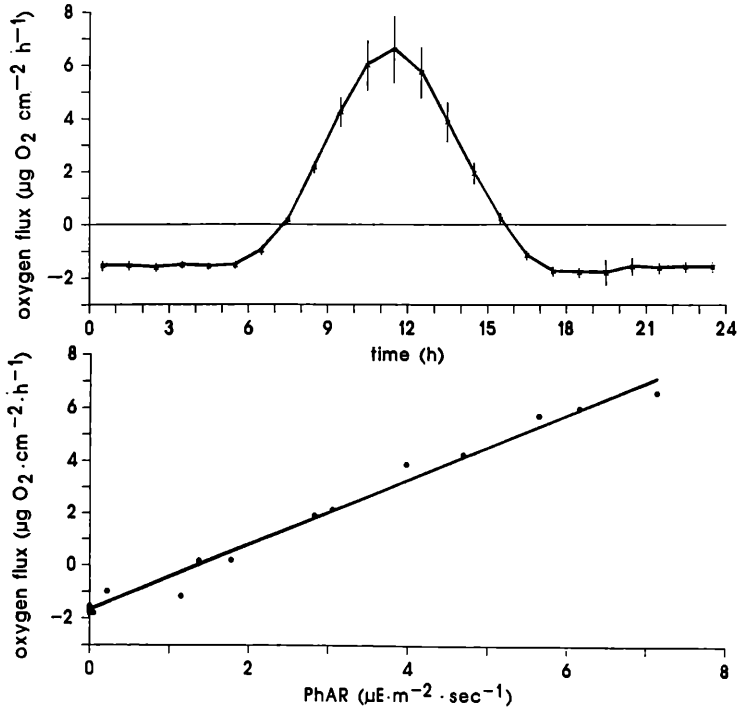


Fig. 15: Daily course of oxygen fluxes in *L. fragilis* at 98 m depth. Changes in oxygen fluxes were continuously monitored on a chart record. The respiration chambers were flushed automatically every 30 min. Top: oxygen evolution as a function of time of day ($n=5$ corals, with SD). Below: In-situ photosynthesis versus irradiance response with regression line (significance $p < 0.001$).

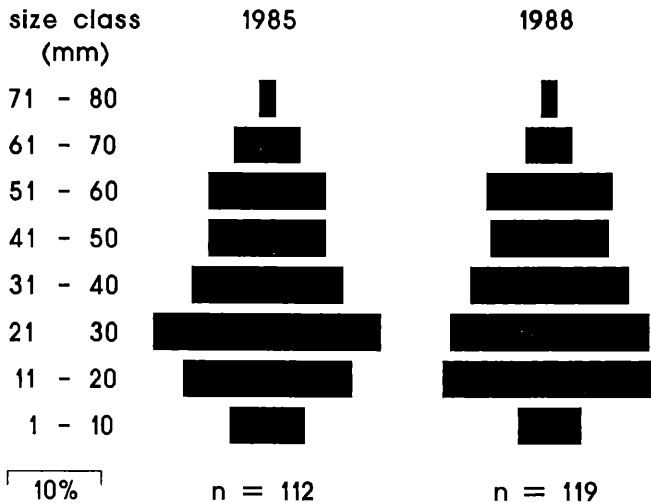


Fig. 16: Size class distribution of *L. fragilis* on a marked test square over a period of 3 years. After 3 years, 7 recruits had appeared on the selected site.

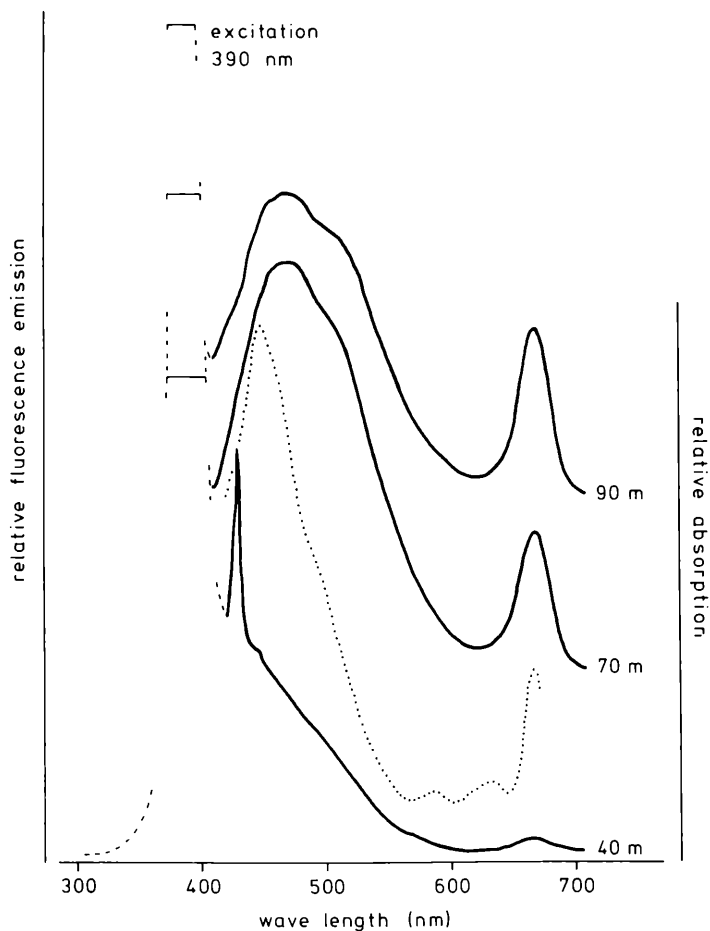


Fig. 17: Fluorescence emission spectra of chloroform extracts including host tissue and algae of 40, 70, and 90 m transplants after one-year exposure at transplantation depth, and absorption spectra of chloroform extracts from zooxanthellae (dotted line). The probes were excited with 390 nm long UV light.

Future and perspectives

In the 19th century the Austrian-Hungarian "Pola" expeditions and the many voyages of famous explorers like FORSSKAL, EHRENBURG, RUEPPELL, or KLUNZINGER unfolded by their pioneering work the highly diverse organismic life inhabiting the Red Sea. In the 20th century, particularly the German research vessel "Meteor" contributed to the knowledge of the life in the deep sea. The twilight zone, however, remained relatively untouched.

I personally regret that our diving operations did not contribute more to the knowledge of organismic life at that depth. One reason is the structure of present-day research funding. Devoted sampling expeditions like those of the 19th century would hardly find a sponsor. The search for processes, mechanisms, and functions of structures are the fashionable modern topics, although we are now aware that biodiversity must be studied not only for the sake of curiosity or to satisfy our morals. The genetic heritage is a valuable resource. Therefore the search for existing biodiversity and the assemblage of a catalog of the long-evolved genetic library is of identical concern as the unravelling of the human genetic code.

The intermediate depths of the oceans are an important path between surface waters and the nutrient-limited deep sea. The energy flow and nutrient transports, but also the organisms and communities, i.e., the conveyers of the processes, are of global interest. They need to be studied more intensively and investments have to be made.

Worldwide, submersibles have proved to be an indispensable tool as an observation chamber, experimental platform, camera window into the deep, or as an effective sampling gear. They allow selective collections and detailed recordings and are not exposed to chance events as most conventional gear is when guided from the surface by a mothership.

In the near future, submersibles and remotely operated vehicles will be the leading techniques to discover new forms of organismic life and the mechanisms of their survival and adaptations in their extreme environments. This is an exciting research front. As "submersible" biologists we dare to participate in this future venture. At the same time, we should also be given more time and funds for extended species sampling to prove the existence of such new forms of organismic life - a task which began more than a century ago when the old-fashioned famous deep-sea expeditions explored the oceans - the first "Pola" expedition to the Red Sea in 1895/96 was one of them.

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