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CORAL REEFS
IN THE PAST, PRESENT AND FUTURE

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Bernard LATHUILIERE & Jörn GEISTER
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CORAL REEFS

IN THE PAST, PRESENT AND FUTURE

held in Luxembourg

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Jointly organized by:
Geologisches Institut der Universität Bern (Switzerland)
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Musée National d'Histoire Naturelle (Luxembourg)
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edited by

Bernard LATHUILIÈRE & Jörn GEISTER

1995

PREFACE

The "Second European Regional Meeting" of the "International Society for Reef Studies" was held from September 6th to 9th, 1994 at the Centre Universitaire de Luxembourg, Luxembourg City under the patronage of His Royal Highness the Grand Duke of Luxembourg. It was inaugurated on the morning of September 6th by H.E. Dr. Marc Fischbach, Minister of Education and Research of the Grand-Duchy of Luxembourg.

Today Luxembourg is a landlocked country situated some 250 km from the nearest coastline. But during much of its Phanerozoic history it was covered by the sea. Beautiful coral communities flourished here 370 million years ago when the Early Devonian sea inundated this area. Some 170 million years ago, in the Middle Jurassic epoch, some of Europe's best developed coral reefs thrived not far from the southern coastline of the former Ardennes Island, known today as the Rhenish Massif. These reefs are well preserved and were the highlight the first day of our pre-meeting field trip in the southern outskirts of the Grand-Duchy at Rumelange.

Coral reefs can be traced through the past several hundred million years of earth history, and are one of our present-day ecosystems with very high species diversity, but they are very susceptible to environmental stress. During the history of earth they were subjected to permanent alterations caused by global changes in the environment. As a result of these stresses, the diversity of coral reefs was reduced and in some cases even whole ecosystems collapsed. Of all the organisms interacting in reefs, corals were those most affected by these environmental changes and thus were the first to disappear under excessive stress. After coral reef ecosystems collapsed in the geological past, they were often replaced by non-anthozoan reefs, such as sponge reefs, bryozoan reefs, and others. In the overall geologic historical perspective non-anthozoan reef ecosystems were even more important than those dominated by corals.

Today, many coral reefs the world over are threatened by the activities of man: dredging and filling operations, toxic effluents from industrial and agricultural developments, sewage pollution causing eutrophication. In addition, we are observing world-wide coral bleaching and the demise of corals as well as the degradation and dying-off of entire reefs that is related to large-scale changes in environmental patterns. Thus, we can speculate that we are approaching again the threshold to another period of coral-free reefs.

We can only really understand the "reefs of the present" by studying the "reefs of the past". Only detailed knowledge of the "reefs of past and present" permits us to speculate about the "reefs of the future". Therefore, the Luxembourg Meeting was appropriately preceded by a three-day field trip to "coral reefs of the past" (Jurassic reefs of Luxembourg and Lorraine) and followed by a ten-day excursion to "coral reefs of the present" (Sinai, Red Sea, Egypt).

Some 140 specialists attending the Meeting at Luxembourg discussed in thematical sessions and workshops all aspects of reef science ranging from fossil to recent reefs. In addition to scientific topics, sessions and workshops were organized to discuss techniques of reef management and monitoring as well as successful utilisation of volunteers in applied marine research and reef management. All these discussions expressed concern in preserving our coral reef heritage for the future. Scleractinian corals still constitute the predominant framework builders of modern reefs. However, their taxonomy is badly in need of revision. To this end, the Luxembourg meeting hosted a workshop of the "International Working Group on Scleractinian Corals".

The Proceedings have been arranged by topic in separate sections for the sessions and workshops. Each manuscript was read by at least two reviewers. The decision to accept or reject manuscripts and to revise them extensively was based on the reviewers' comments. We are grateful to the reviewers for their assistance. Their names are listed elsewhere in this volume. Not all participants were able to submit manuscripts to the Proceedings within the proposed time limits. However, to indicate the entire spectrum of contributions to the meeting the editors decided to also publish the abstracts of those authors who did not submit a full article. These abstracts were not reviewed but were checked for any typographic and stylistic errors. In spite of these efforts, many errors undoubtedly remain and the editors apologise for these.

This meeting was made possible through the joint effort of many individuals and organisations. It is a pleasure for the Organisation Committee to acknowledge their help and support in planning and holding the meeting. In particular, we thank Ian G. Macintyre (Washington, D.C.) for his encouragement to organize the meeting, Pierre Seck (Luxembourg) for hosting it at the Centre Universitaire, and the organizers of the workshops and the technical staff of both Centre Universitaire and Museum for their untiring help during the sessions. The organisation committee is also grateful to our four sponsors: The International Science Foundation (Washington, D.C), Musée National d'Histoire Naturelle (Luxembourg), Centre Universitaire (Luxembourg), and Service Géologique (Luxembourg). Last but not least, the organizers want to extend their cordial thanks to all the members of the international coral reef community who gathered at Luxembourg in the "green heart of Europe", once inundated by tropical seas, which they - through their vivid and active participation - transformed again for a few days into the pulsating heart of the coral reef world.

Bernard Lathuilière and Jörn Geister

Vertical reef wall at "Ras Umm Sid", Sinai (Red Sea) overgrown by soft corals, scleractinians and *Millepora*, viewed at about 4 meters of water depth. Red fish are *Anthias squamipinnis*.
Visited during the Post-Meeting Snorkeling Trip to "Coral Reefs of the Present". Photograph: J. Geister.

Above: Panoramic view from "Ras Umm Sid" lighthouse to the bay of Sharm-el-Sheikh, Sinai (Red Sea). Shallow fringing reef (foreground) attached to a coastline of Pleistocene reef limestone forming vertical coastal cliffs (background).

Below: Reef slope at "Thomas Reef", a platform reef in the Strait of Tiran (northern Red Sea) viewed from about 3 meters of water depth. Red fish are *Anthias squamipinnis*.

Both localities were visited during the Post-Meeting Snorkeling Trip to "Coral Reefs of the Present".
Photographs: J. Geister.

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QUATERNARY REEFS AND RELATED ENVIRONMENTS

CORAL REEFS AT GANGEHI (NORTH ARI ATOLL, MALDIVE ISLANDS)

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Abstract - The main features of subtidal zonation were described through diving surveys down to about 35 m, in a total of 14 sites. Three major environmental units were investigated: the walls of the passes connecting the lagoon with the ocean; patch reefs within the pass; patch reefs within the lagoon and the lagoonward side of the faros. Caves, notches and other erosional morphologies were seen at various depths in all of the three units. Each unit presented its particular zonation and organism assemblages. Such zonation patterns appeared to be essentially under hydrodynamic control: in zones with strong currents *Tubastraea micranthus* and other rheophilic, strictly planktotrophic forms extended into shallow depths, substituting for algae and zooxanthellate corals even in well-lit situations.

1. INTRODUCTION

The Maldives are one of the biggest groups of atolls in the world and have attracted the interest of scientists since Darwin's time (ANDERSON 1991). However, only four, out of more than 20 atolls, have been the subject of extensive research: Addu (STODDART 1966), Felidu (CIARAPICA & PASSERI 1993), North Malé (MATTEUCCI & RUSSO 1985; CIARAPICA & PASSERI 1993), and Rasdu (SCHEER 1974).

Ari is one of the largest atolls in the Maldives and is situated on the western side of the archipelago; it was touched by the Xarifa expedition in 1957-58 (SCHEER 1971; PILLAI & SCHEER 1976) and since then no further field work has been done on it. Ari has been proposed as a Biosphere Reserve (KENCHINGTON 1983), and the need of basic data for proper management has been advocated. Such a need is becoming urgent due to the present concern about pollution and human impact on Maldivian reefs (SHEPHERD *et al.* 1992; RISK *et al.* 1994).

We visited Ari Atoll in February and April 1989. A number of biological surveys, using SCUBA diving, were performed in the north-west part of the atoll, around the island of Gangehi, a tourist resort. Ecological information on deeper reefs in the Maldives is poor compared to that on reef flats (SHEPPARD & WELLS 1988). So we paid particular attention to the main features of subtidal zonation down to about 35 m.

2. MATERIALS AND METHODS

2.1. Study site

The Ari Atoll is notable for its ring-shaped reefs, which form the perimeter of the atoll in place of the more usual continuous, linear reef flat (SHEPPARD & WELLS 1988); these ring-shaped reefs are called faros (from the Maldivian term *faru*: ANDERSON 1991). The western border of the atoll, facing the ocean, has large scattered faros separated by wide (*kandu*) or narrow (*kanduolhi*) passes, connecting the open sea with a lagoon (*mudu*) more than 50 m deep (Fig. 1).

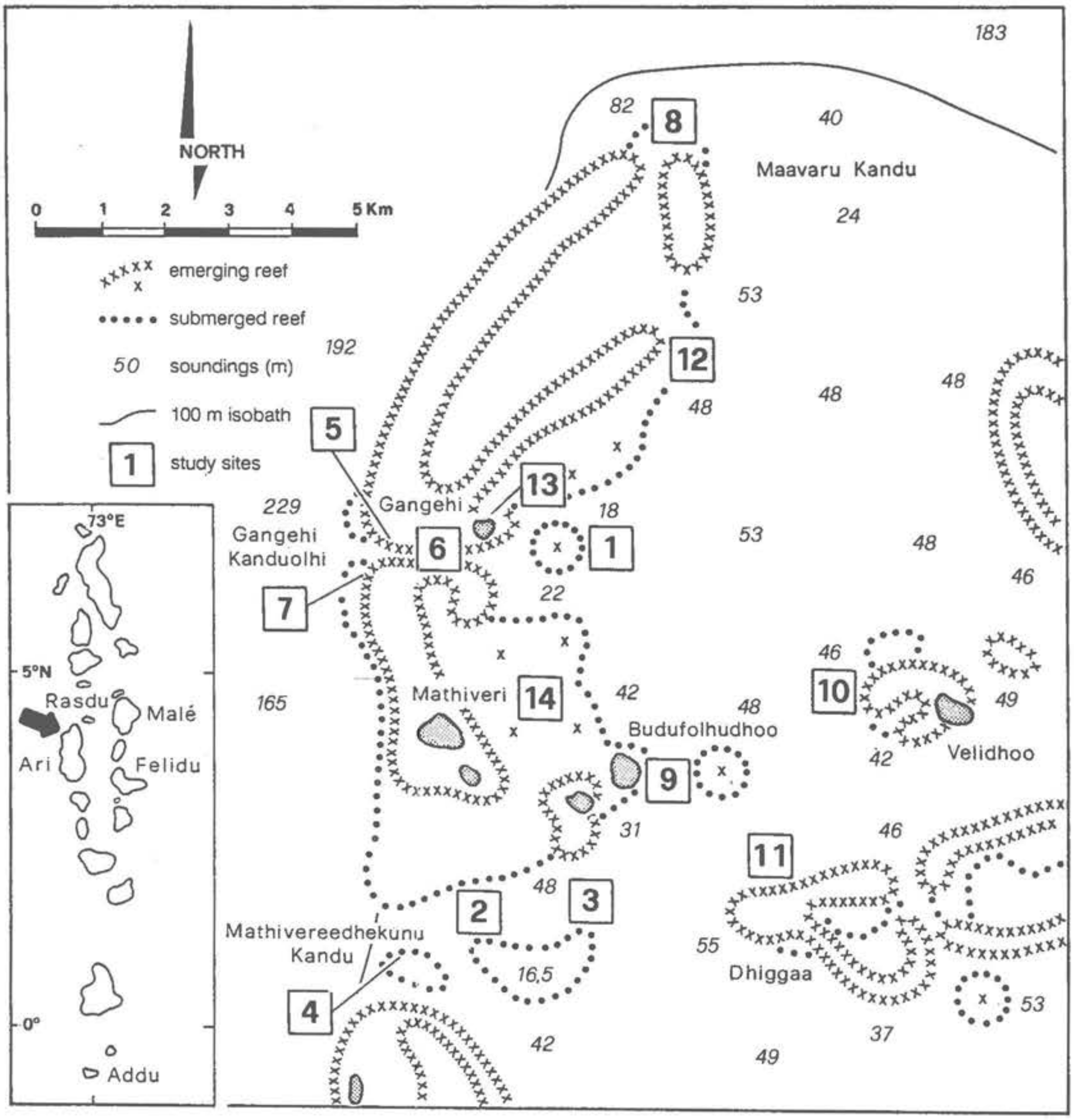

Fig. 1. The Maldives (arrow indicates study area) and the north-west part of Ari Atoll, with location of diving survey sites.

Faros often support low islands, rising not more than a few meters above sea-level. The island of Gangehi is situated on the Northeast faro of the west rim of Ari Atoll.

It is a very small island (about 7500 m^2), facing the lagoon to the North and a pass (the Gangehi kanduolhi) to the South (Fig. 2).

Site names used in this paper follow the Map of Maldives (edition 1979) and British Admiralty Chart No 1013 (edition 1993). Sites not indicated on these maps were named according to usage by local people or tourist guides.

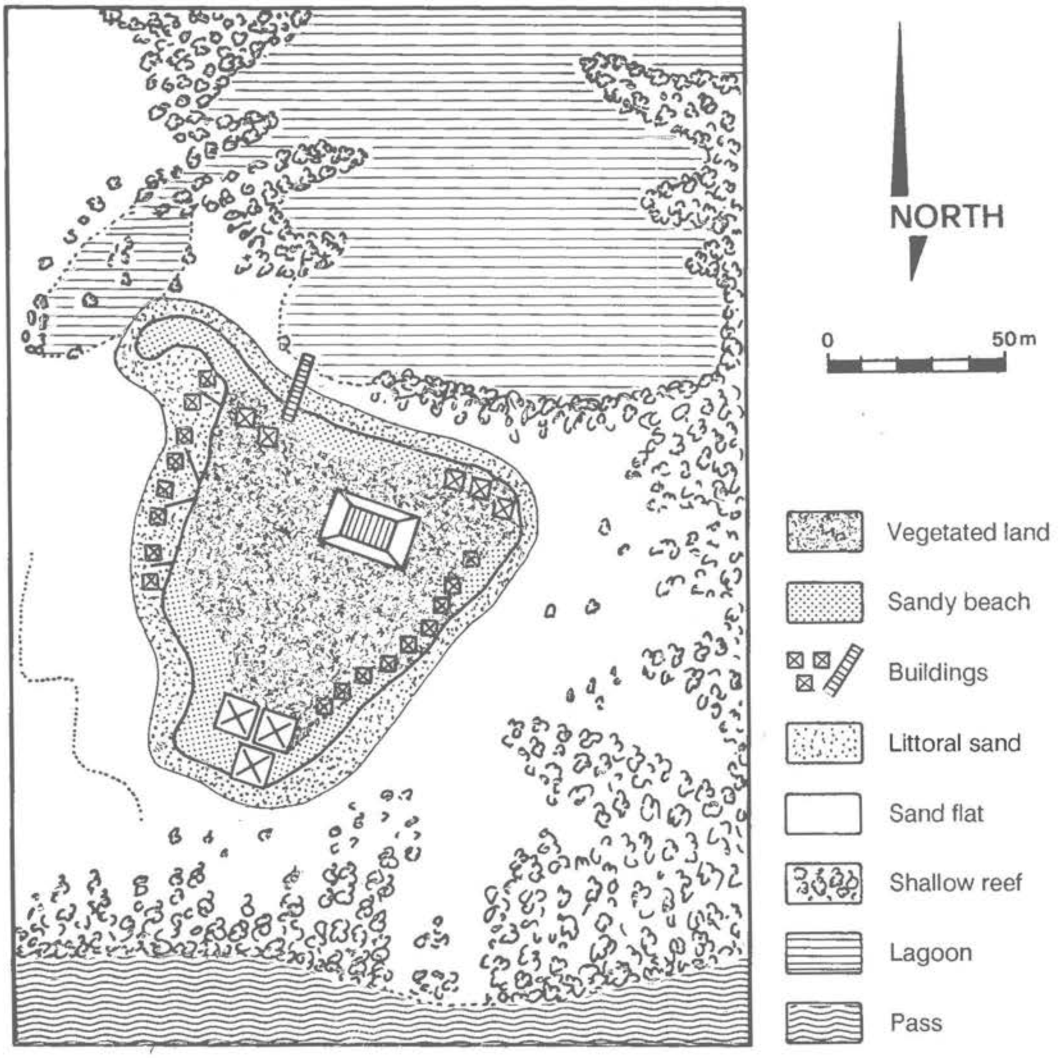

Fig. 2. The island of Gangehi.

2.2. Field work

Topography of the island was surveyed by compass traverse and pacing, forming a closed circuit (STODDART 1978), and was perfected with oblique aerial photographs.

Underwater work was done at 14 sites by SCUBA (sites 1 to 5, 7-8, and 12) or skin diving (sites 6, 9 to 11, and 13-14); all sites were visited at least twice. When possible, dives were carried out along transects perpendicular to the reef edge. Depth was measured by diving computer, exposure by compass, and substrate inclination by a hand-made clinometer (GAMBLE 1984). Biological zonation was described through the physiognomic method used by BIANCHI *et al.* (1991; see also BEARD 1978).

3. RESULTS

Das Kurani Thila (site 1: Fig. 3) - *Thila* is the Maldivian word for a pinnacle reef not reaching the surface. The top of the pinnacle, at about 10 m depth, exhibited a mixed coral assemblage; the green alga *Tydemania expeditionis* was abundant. Towards the edge, table-shaped *Acropora* was found superimposed upon this assemblage. The northern slope (inclined 45° on average) was dominated by *Acropora formosa* down to about 19 m depth. After a narrow terrace covered with sand, mixed corals again dominated down to a sandy floor at the base of the pinnacle (26 m depth): massive (*Diploastrea heliopora*), brain (*Platygyra daedalea*) and bubble (*Physogyra lichtensteini* and *Plerogyra sinuosa*) corals were particularly abundant. The northern slope was steeper (70°): hermatypic corals were unimportant, and the community was characterized by sponges (*Homaxinella* sp., *Acanthella carteri*, *Spirastrella* sp.), wire corals (*Cirripathes anguina*), and gorgonians (*Acabaria* and others). Small caves were seen at 19 m. Above 12-15 m green algae (*Tydemania*, *Halimeda*, *Udotea*) and leather corals (*Sarcophyton*) dominated.

Nika Thila I (site 2: Fig. 3) - It was located on the western corner of a submerged patch reef elongated in the W-E direction. The top, at 14 m, was covered by tables of *Acropora hyacinthus*, together with small coral heads and leather corals. The NE side was very steep, although interrupted by narrow terraces at 19 m, 23 m, and - less pronounced - 30 m depth. Major inhabitants of the vertical tracts were hydroids (*Macrorhynchia phoenicea*), crinoids, sponges (*Homaxinella*), soft corals (Nephtheidae), and wire corals (*Cirripathes anguina*). The thila ended at about 33 m on a sandy bottom. The SW side was less steep (60° on average) and had no terraces, but caves opened at about 25 m depth. The major organisms found in the caves were small gorgonians (*Acabaria*) and black corals (*Antipathes*). Outside the cave, a change in community composition was observed at about 22 m depth: above, gorgonian, sponges and encrusting corals (*Pachyseris speciosa*) were dominant; below, *Tubastraea micranthus* was extremely abundant.

Nika Thila II (site 3) - Site 3 was located on the same elongated patch reef of site 2, but at the eastern corner. The northward-facing slope was covered by *Tubastraea micranthus*. Between 20 and 28 m depth there were several erosional morphologies (caves, notches, windows, balconies). The caves were inhabited by black corals (*Antipathes*) and soft corals (*Scleronephthya*); immediately outside, gorgonians, crinoids, hydroids (*Macrorhynchia phoenicea*) and sponges (*Homaxinella*) were present.

Mathivereedhekunu kandu (site 4: Fig. 3) - It is a pinnacle reef within a large pass. The top, at 14 m depth, was sandy with scarce coral cover and some algae. Mixed corals (brain corals, small *Acropora* heads, etc.) and leather corals (*Sarcophyton*) were present on the northern rim. The slope (inclined at 45°) was dominated by

Tubastraea micranthus from 20 m to the maximum depth explored (35 m): the great water transparency allowed estimates of its dominance downward to at least 50 m. Between 22 m and 28 m depth the slope was interrupted by a series of caves: the roof was inhabited by *Scleronephthya corymbosa* and large *Antipathes dichotoma*, the floor mainly by gorgonians (*Subergorgia*, *Ellisella*, *Junceella*). Wire corals, Nephtheidae, *Macrorhynchia phoenicea*, *Filograna* and other rheophilic forms were abundant at the cave entrances.

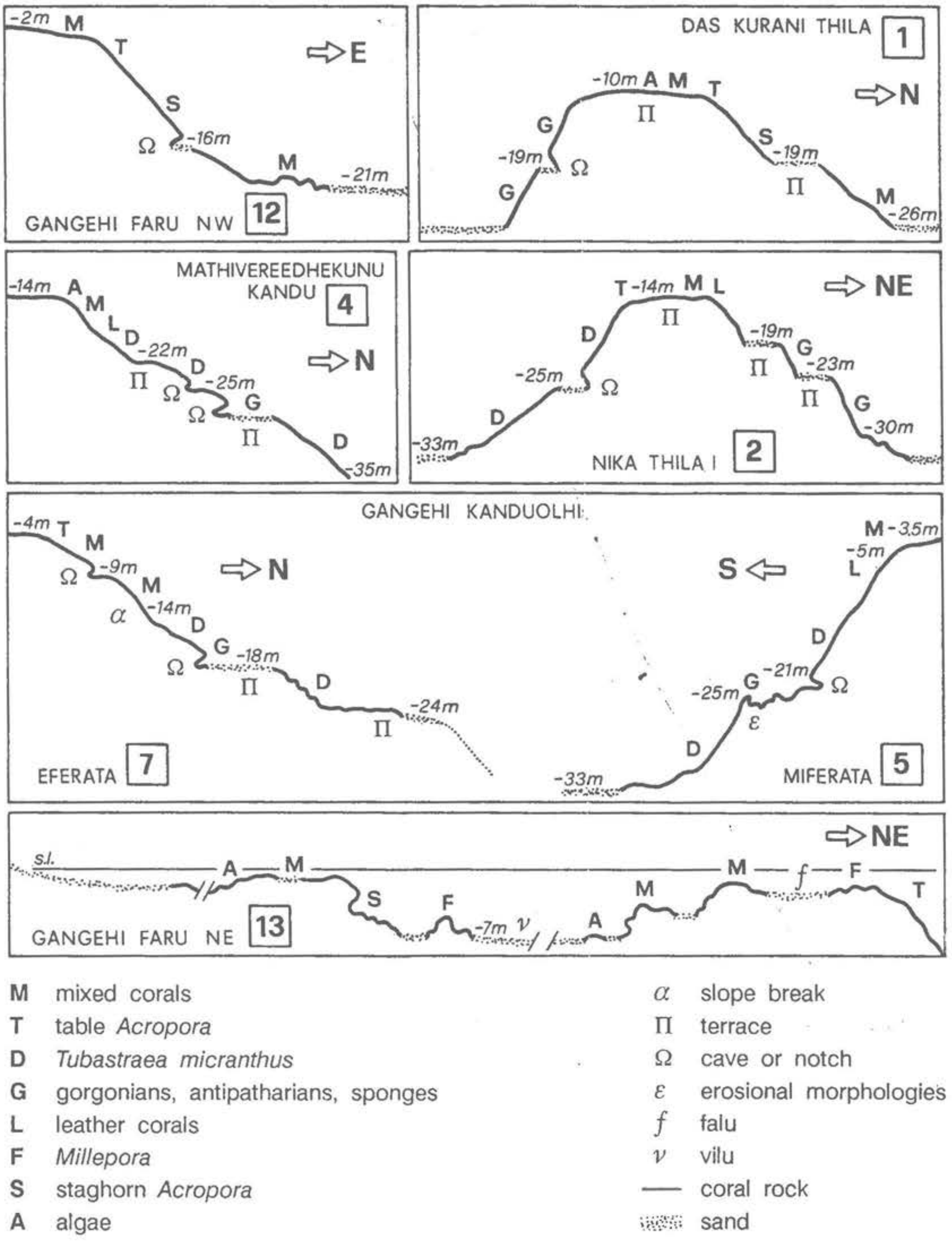

Fig. 3. Representative profiles at some study sites (numbers in boxes).

Gangehi kanduolhi miferata (site 5: Fig. 3) - *Miferata* is the Maldivian expression to mean "this side" (of the pass, with regard to Gangehi Island). Dives were done near the oceanward mouth of the pass. The reef top was at about 3.5 m and was covered by leather corals and coral heads; small gorgonians (*Acabaria*) were extremely common within reef crevices. A strongly inclined (60°) slope started at 5 m and *Tubastraea micranthus* was dominant from 10 m depth downward. Caves, notches and other erosional morphologies were present between 21 and 25 m depth. Gorgonians (*Subergorgia* and others) and antipatharians added to *T. micranthus* on the lower slope down to the sandy floor, at 33 m.

Gangehi faru South (site 6) - It is situated near the lagoonward end of the Gangehi kanduolhi. Three zones were recognized on the flat, from the island to the reef edge: mixed corals, sand flat, and *Millepora* zone. The upper slope was covered by table corals. Below, coral spurs were recognizable.

Gangehi kanduolhi eferata (site 7: Fig. 3) - *Eferata* means "that side": site 7, indeed, was facing site 5. The slope had a mean inclination of 50° down to about 14 m, and was inhabited by mixed corals with rare *Acropora hyacinthus*, especially on the upper slope (around 4 m depth). Notches occurred at 9 m. Below 14 m, the inclination was 40° and some sand was present; *Tubastraea micranthus* was the dominant species. Caves with antipatharians were found at 18 m; below, and down to a terrace at 24 m, many sponges, large gorgonians (*Subergorgia mollis*), Nephtheidae, and whip corals (*Junceella rubra*) added to *T. micranthus*.

Mahavaru kandu (site 8) - A wide terrace at 10 m depth, in continuity with the northern rim of Gangehi faru, borders the western side of this large pass. Huge massive *Porites*, together with leather corals and some encrusting corals, characterized the assemblage on the terrace. The bases of the huge *Porites* colonies were greatly eroded, forming cavities in which thrived gorgonians (*Subergorgia*, *Acabaria*), Nephtheidae, and hydroids. The terrace gently sloped northward, with a series of steps on which sand and massive corals (*e.g.*, *Diploastrea heliopora*) alternated.

Budufolhudhoo (site 9) - The reef edge and the upper slope were inhabited by table *Acropora*, and the slightly inclined slope, with spurs and grooves, by *Acropora formosa*. Caves were present at 8-12 m. The slope ended at about 15 m on sand.

Velidhoo (site 10) - The northern rim of the reef flat had a rich assemblage of mixed corals and table corals. The slope had a spur-and-groove system, with staghorn *Acropora* chutes in the grooves. The north-west rim exhibited dead corals, covered by the ascidian *Didemnum molle*, and leather corals (*Sarcophyton*).

Dhiggaa (site 11) - Mixed corals, with *Porites* and *Acropora* heads, characterized the reef flat, whereas staghorn *Acropora* monopolised the edge and the upper slope. A peculiar trait was the abundance of echinoderms (*Bohadschia graeffei*, *Culcita novaeguineae*, *Heterocentrotus mammillatus*, etc.).

Gangehi faru north-west (site 12: Fig. 3) - The reef top, at 2-3 m depth, had mixed corals, with some table *Acropora* toward the edge. The slope down to 13 m was occupied by a belt of living *Acropora formosa*. Below, grooves with *Acropora formosa* chutes alternated with spurs covered by foliaceous and other corals. A small cave was present at 16 m depth. The slope ended at 21 m on sand, with isolated small patch of massive corals (*Favia speciosa*, *Montipora* sp., *Diploastrea heliopora*).

Gangehi faru north-east (site 13: Fig. 3; see also Fig. 2) - The beach of the island continued underwater with a sandy floor with holothurians. An algal zone followed, with numerous species of both phaeophyceae (*Padina gymnospora*, *Turbinaria ornata*) and, especially, chlorophyceae (*Codium* sp., *Dictyota dichotoma*, *Dictyota indica*, *Halimeda incrassata*, *Halimeda moniliformis*, *Halimeda platydisca*, *Udotea orientalis*). Then, a shallow reef with mixed corals faced a lagoonal tract (called *vilu*) reaching 7 m depth: the slope was covered by *Acropora formosa*, while on the sandy floor of the lagoon algae and small coral patches with branching *Porites* and *Millepora* occurred. A larger reef tract, dominated by mixed corals, nearly reached the surface and further extended northward: a very shallow sandy lagoon (*falu*) was present in its middle. The outer edge exhibited a series of narrow belts: *Acropora* rubble, living staghorn *Acropora*, mixed corals, and then *Millepora*; *Acropora* tables were conspicuous on the upper slope.

Mathiveri faru (site 14) - The lagoon side of the reef had a strongly inclined slope, with a spur-and-groove system down to about 15 m depth; below, the inclination was slighter. *Acropora formosa* characterized the grooves.

4. CONCLUSIONS

Two major benthic assemblages can be distinguished on the coral reef around Gangehi: the first is photophilic and - at least in part - autotrophic, being composed by algae and zooxanthellate anthozoans (either hermatypic scleractinians or leather corals); the second is sciaphilic and exclusively heterotrophic, consisting of non zooxanthellate species, such as sponges, gorgonians, antipatharians, and ahermatypic corals. It should be noted that, although deprived of zooxanthellae, *T. micranthus* is considered hermatypic by SCHUHMACHER (1984) due to its constructional ability.

These two assemblages largely correspond to the two biocoenoses that PICHON (1978) called "reefal" and "subreefal", respectively, and substituted for each other according to depth and substrate inclination, but their detailed composition and zonation were different according to the sites. Three major units can be recognized in this respect: 1) the walls of the oceanward mouth of the passes; 2) patch reefs (thila) within the pass; 3) thila within the lagoon and the lagoonward side of the faroes.

In the first situation, the reefal biocoenosis was dominant above 10 m depth and was often represented by leather corals. The formation of assemblages dominated by leather corals was considered related to disturbance by DAY (1993). Below 10 m, the subreefal biocoenosis became dominant, especially with *Tubastraea micranthus*.

On the thilas within the passes, the most striking aspect of the reefal biocoenosis was constituted by large tables of *Acropora hyacinthus*. *Tubastraea micranthus* and the rest of the subreefal biocoenosis appeared only below 20 m depth.

Lagoon reefs exhibited *Acropora formosa* belts (and chutes) - already described by SPENCER DAVIES *et al.* (1971) at Addu - as a major feature of the reefal biocoenosis. The fact that they were present with similar features on both the back and the front reef is reminiscent of the zonation model proposed by GEISTER (1983) for the Caribbean; a similar zonation pattern was exhibited by the algae (see also TSUDA & NEWHOUSE 1966, and CIARAPICA & PASSERI 1993). In deeper areas of lagoon reefs, the subreefal biocoenosis was usually absent: large massive corals (especially *Diploastrea heliopora*) were dominant, always belonging to the reefal biocoenosis.

In virtually all of the three environmental units, submarine terraces, caves, notches and similar erosional morphologies were common at various depths: they are evidences of sea-level changes (GUILCHER 1988). After the sea-level drop at the Plio-Pleistocene boundary, the Holocene melting of ice caused a sea level rise. Maldivian reefs were eroded and karstified during emersion periods, originating complicated geomorphologic patterns (CIARAPICA & PASSERI / 1993). Abrasion terraces and corrosion notches can be considered signs of stops and fluctuations within the general transgression trend: depth differences within sites might indicate independent geological history of distinct reefs. The organism assemblage found in caves - described by BIANCHI & MORRI (1994) at Felidu - can be regarded as an enclave of the subreefal biocoenosis, with the absence, however, of *T. micranthus*.

The substitution of subreefal biocoenosis for reefal biocoenosis with depth was not observed in the lagoon; near the lagoon side of the passes, it was observed at 20 m, while near the ocean side of the passes, at 10 m. On reef fronts, this boundary can be as deep as 100-110 m, according to light penetration (FRICKE & SCHUHMACHER 1983). In the channels of Aldabra Atoll, BARNES *et al.* (1971) also observed the displacement into shallow waters of *Tubastraea micranthus* (as *Dendrophyllia micrantha*).

The fact that the boundary between reefal and subreefal biocoenoses is shallower in the passes - where tidal currents are nearly constant - suggests that it is, at least in part, under hydrodynamic control. The importance of water movement in coral reef zonation has been long recognized (ROSEN 1975; GEISTER 1977), but emphasis has mainly been placed on waves rather than on currents (DONE 1983).

In zones with strong currents, *T. micranthus* and other rheophilic, strictly planktotrophic forms, can extend into shallow depths, substituting for phototrophic species (zooxanthellate corals and algae) even in well-lit situations.

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PRODUCTION OF CRYPTOCRYSTALLINE CARBONATE IN AN EXTREME ENVIRONMENT: THE DEEP GLACIAL RED SEA

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Abstract - Pelagic oozes in modern oceans form dominantly by accumulation of coccolithophore remains. In shallow carbonate banks production of cryptocrystalline sediments is more diverse (skeletal disintegration, bioerosion, microbial cementation) and includes products of physico-chemical precipitation ("whitings"). Adjacent to shallow banks, these products mix with pelagic material in periplatform oozes.

Holocene sedimentation in the Red Sea basin is of the pelagic type. Circulation patterns are antiestuarine because rates of evaporation are high. During the last glacial maximum (13 to 25 ky before present) water exchange with the Indian Ocean was reduced and high rates of evaporation resulted in extreme surface water salinities, exceeding the thresholds for the shallow reef systems and most plankton taxa. The sedimentary record of this period is a lithified and finely laminated carbonate crust of 0.5 m thickness, with input of shallow water derived material being negligible, even very close to the reef buildups. Because of the wide bathymetric range (500 to 2700 mbsl) of the hard layer, it is considered to have formed in a deep water environment. Individual laminae of the crust consist of cryptocrystalline carbonate, mainly as aragonite spherulites, Mg-calcite peloids, anhedral mosaics of Mg-calcite and laminated "cryptalgal" fabrics. Their interlocking relationships indicate precipitation at the sea floor. Morphological similarity with previously published microfabrics give some hints on a microbial mediation. This type of benthic carbonate production is not known from present oceans, but may be of importance in order to explain basinal limestones of the sedimentary record dating before the radiation of calcareous nannoplankton. The absence of a planktonic carbonate sink in those examples may have triggered benthic precipitation.

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SEDIMENTATION ON THREE CARIBBEAN ATOLLS, BELIZE, CENTRAL AMERICA

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Abstract - The chief mode of carbonate sedimentation on the Belizean atolls Glovers Reef, Lighthouse Reef and Turneffe Islands is the accumulation of organically-derived particles. Variations in the distribution of the composition and grain-sizes of surface sediments, collected along transects across the atolls, are environmentally controlled. Two major sediment types may be distinguished.

(1) Reef and fore reef sediments are dominated by fragments of coral, coralline algae and *Halimeda*. Mean grain-sizes range from 1-2 mm.

(2) Back reef sediments contain more mollusk fragments, more fine- grained sediment (<125 μm) and appear to have fewer *Halimeda* fragments. In addition, sediments from inner platforms and shallow lagoonal parts of Glovers and Lighthouse Reefs comprise non-skeletal grains, namely fecal pellets. Sediments from lagoonal patch reefs may contain up to 20 % coral fragments. Mean grain-sizes range from 0.1-1 mm and are finest on the inner platform and lagoon floor of the back reef environment.

Within the reef and fore reef environments, it is not possible to distinguish sub-environments on the basis of textural and compositional differences of the sediments. Sediments from patch reefs contrast with those from back reef lagoons and inner platforms and are similar in terms of grain-sizes and compositions to reef and fore reef surface sediments.

Non-skeletal grains forming in shallow parts of the back reef in Glovers and Lighthouse Reefs are interpreted to be indurated by interstitial precipitation of calcium carbonate from warm, supersaturated water flushing the sediment. The lack of hardened non-skeletal particles in the back reef sediments of Turneffe Islands is most probably due to the abundance of muddy, organic-rich sediment in the well-protected lagoon. Fine sediment is less permeable and organic films prevent cement overgrowth on particles.

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THE QUATERNARY CORAL REEF TRACTS OF HATERUMA (RYUKYU ISLANDS, JAPAN)

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Abstract - The island of Hateruma is located at the southwestern end of the Ryukyu Island chain and covers an area of about 15 km^2 with its highest point at 59.5 m.a.s.l.. The morphology of Hateruma is characterized by an eight step staircase (I to VIII after OTA *et al.* 1982) most of which eroded into the previously formed coral reefs (II and IV to VIII). This study presents 100 age estimations on 43 coral samples using electron spin resonance (ESR), alpha- and mass spectrometric U-series methods. The dating results imply that the Ryukyu Limestone was predominantly formed during oxygen isotope stages 7 and 5e. Two age estimates of around 300 ka suggest an earlier reef-building period. The main problem for establishing the Quaternary history of Hateruma lies in the fact that the coral ages and the staircase morphology do not correlate. Additionally, it is difficult to distinguish autochthonous from allochthonous samples, the latter may have been relocated by tsunamis. Corals relating to substages 5a and 5c (around 75 and 105 ka, respectively) are found in the immediate vicinity of much older samples. The results of this study prove the disappointing fact that Hateruma cannot yet be used as a tool for reconstructing palaeo sea-levels.

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THE HERMATYPIC CORAL FAUNA OF SUBTROPICAL SOUTH-EAST AFRICA

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Abstract - An overview and a check-list are given of all hermatypic corals occurring in South Africa and subtropical southern Mozambique. This is the first complete account of this area's coral fauna. The South African hard coral fauna consists of 90 species in 41 scleractinian genera, 1 stoloniferous octocoral genus (*Tubipora*), and one hermatypic hydrocoral genus (*Millepora*). It is poorer than the fauna of southern Mozambique with 117 species in 44 scleractinian genera, 1 stoloniferous octocoral (*Tubipora*) and 1 hydrocoral (*Millepora*).

Particularly the Acroporidae and Fungiidae are better represented in Mozambique than in South Africa (Acroporidae: 30/22 species, Fungiidae 9/5 species).

The reason for the richer coral fauna in Mozambique lies in the greater ecological differentiation of its reefs. In South Africa, there are no true coral reefs but fossil sand dunes and beachrock platforms covered with corals. These do not reach the water-surface and do not form typical reef environments such as lagoons, reef crests, and reef slopes. Most typical lagoonal coral species (like many branching *Acropora*) have therefore their southern limit at Inhaca Island, Mozambique.

The southern distribution limit of hermatypic coral genera in Africa is at 27°54'S, on Leadsman Shoal, Natal Province. Only localised coral outcrops are found further south.

In comparison with other subtropical coral reef areas in similar latitudes, the South-East African coral fauna is of average richness (subtropical Western Australia: 201, subtropical Eastern Australia: 118, northern Red Sea: 134; Ryukyus: 363 species). The number of species recorded in southern Mozambique (115) is the highest yet recorded on the African coast outside the Red Sea (tropical East Africa: 112).

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PLEISTOCENE REEFS IN SINAI: EUSTATIC AND CLIMATIC CONTROLS

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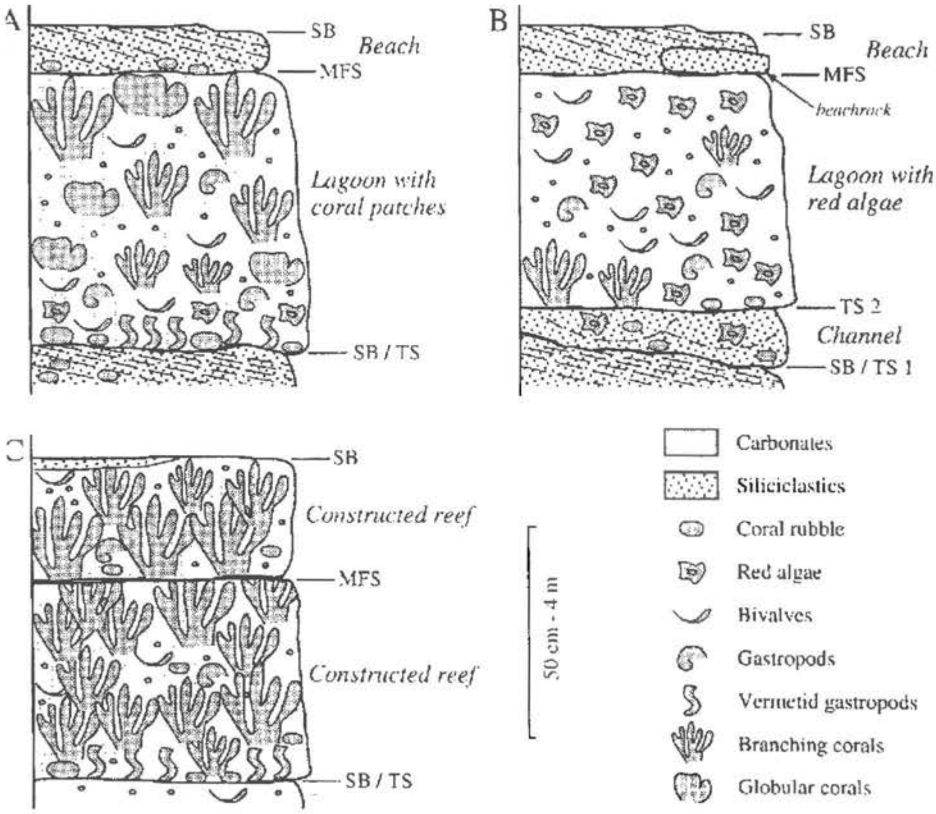
Abstract - Uplifted Pleistocene reef sequences have been studied in the surroundings of Sharm-el-Sheikh and Naama Bay in southern Sinai, Egypt. Two reef terraces are well developed: the higher one reveals U/Th ages between 350 and 270 ka B.P. and thus corresponds to the interglacial period of isotope stage 9, the lower one, dated between 140 and 60 ka, to that of isotope stage 5. Reefs formed during isotope stage 7 occur only locally in the studied area.
The reef terraces exhibit, despite strong tectonic uplift and tilting, well preserved small-scale depositional sequences. Constructed coral thickets of fringing reefs, coral patches in lagoons, or lagoonal facies dominated by red algae are associated to a rapid rise of relative sea level, the transgressive surface (TS) commonly being underlined by reworked coral pebbles and vermetid gastropods. The maximum-flooding surface (MFS) is well marked in lagoonal settings where siliciclastic beach sands prograde over it (Figs A and B), but may be more difficult to identify in open reef facies, where coral

growth continues during sea-level highstand (Fig. C). Prograding siliciclastics suggest that accommodation space diminishes. The sequence boundary (SB), corresponding to a fall of relative sea level, then caps the small-scale sequence. Reef growth is thus restricted mainly to transgressive phases, whereas the corals are killed by siliciclastic input during phases of high and lowering sea level.

Sea-level high stands correlate with rainy periods in the hinterland, and therefore with increased terrigenous run-off. These periods are in tune with the shifting of monsoonal belts and, consequently, with insolation changes in the Milankovitch frequency band. The observed depositional sequences thus result from eustatic as well as from climatic fluctuations.



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PETROSTRATIGRAPHIC ANALYSIS OF HOLOCENE REEF CARBONATES, TAIWAN, R.O.C.

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Abstract - A variety of reef carbonates has been recognized in the Holocene raised reef of south Taiwan. The formation of these reef carbonates is complex. The carbonate was formed generally by a mixture of four different elements: 1. biogenetic frameworks of different types ; 2. loose sediments formed by destructive processes ; 3. cryptic encrusting organisms which consolidated the debris and loose skeletons to form secondary frameworks ; 4. cementations of different types. Detailed analysis of these elements, as the growth pattern of organisms, the manner of their attachment, the nature of destruction, transportation and sedimentation, the sequence of precipitation of cements etc., allow us to establish the process and the timing of reef carbonate formation.

Different processes operate to varying degrees in reef construction. These processes are mainly: I. Biological constructive processes, II. Destructive processes, III. Sedimentological processes, and IV. Diagenetic processes. This paper deals only with destructive processes and the timing of reef carbonate formation.

Bioerosion was observed only in some part of the reef carbonates. Bioerosion of dead coral by boring bivalves, sponges and algae was intensive.

Physical destruction is important: 1. Organic debris deposits are generally caused by waves and currents. 2. Major destruction is caused by earthquakes, typhoons or palaeofloods which occur only sporadically and periodically. They can be demonstrated by tempestites or palaeoflood deposits which deposited generally in interstices between reef bodies.

Tempestites are very common in reef carbonates. These are typically demonstrated by broken organism fragments of different sizes which generally show graded bedding suggesting a deposit of a turbid suspension caused by a storm of short duration.

Palaeoflood deposits are also very common. The beds are characterized by broken organic fragments of different sizes with important mud content.

Deposits caused by earthquakes are rare but do exist. They are characterized by large blocks of Pleistocene age cemented organically by Holocene reef carbonates.

The formation of the reef carbonate can be very complicated. Detailed petrostratigraphical analysis of reef carbonates demonstrate that the developmental sequence of the reef carbonates can be easily reconstructed stage by stage. Figure 1 shows the petrostratigraphic history of the Shihchu profile which demonstrates that the reef carbonate was formed under different conditions and was constantly modified by mechanical destructions and biological constructions at different stages of biological growth during its formation. This example allows us to establish the general process and the timing of reef carbonate formation. In a general way, it can be summarised as follows:
Stage 1: Construction + minor cementation. Stage 2: Destruction + transportation. Stage 3: Sediments deposited in interstices or cavities + minor cementation. Stage 4: Secondary consolidation + minor cementation. Stage 5: Late cementation of different types found in different environments.

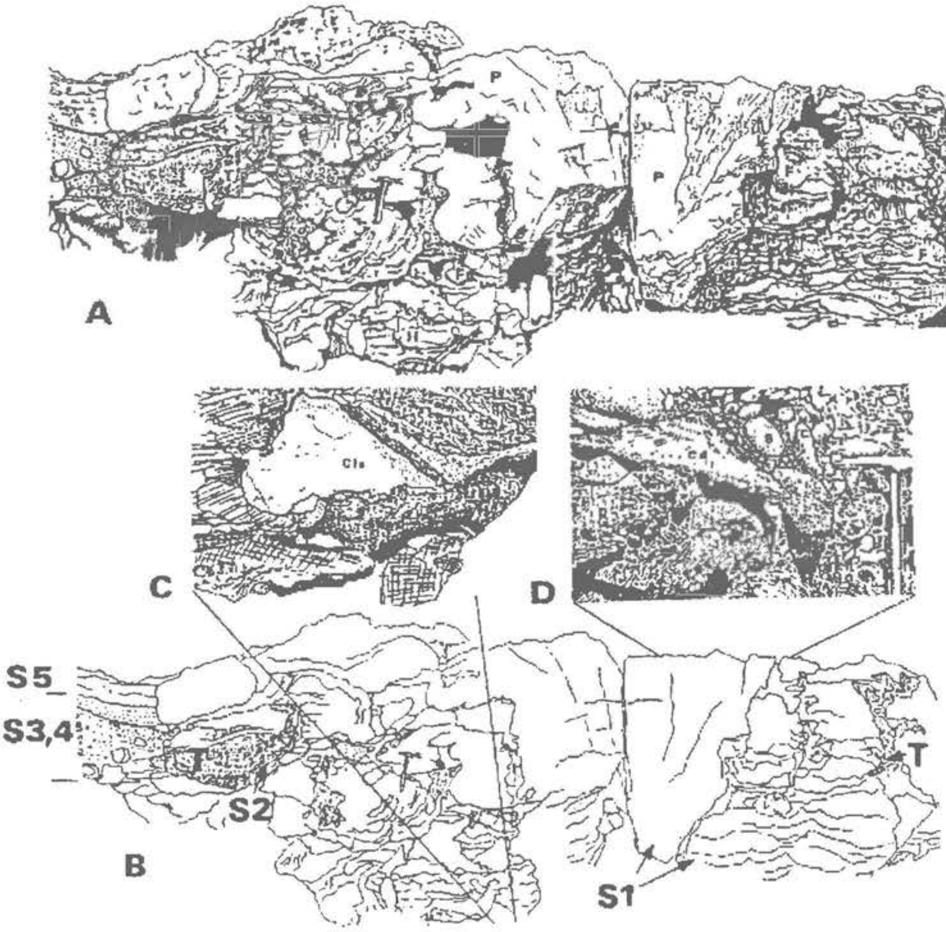

Fig.1 **A.** Shichu profile clearly demonstrates that the reef limestone has developed under varying conditions in different stages during its formation.

B. Microstratigraphical analysis of this profile suggests a developmental sequence of the reef carbonate as follows. Stage 1: Colonisation of massive corals to form an irregular reef carbonate body. Stage 2: Consolidation of reef framework as demonstrated by the development of encrusting corals (*Turbinaria peltata*) on the massive coral colonies. Stage 3: Colonisation of massive and branching corals in different localities. Stage 4: Destruction of these coral colonies by typhoons and storms to form a tempestite (T) which deposited in interstices of the reef framework. Stage 5: Colonisation of lamellar and other organisms which cover and stabilise debris to form a very complex reef carbonate.

C. Weakly attached in situ funnel shaped corals that grew near by on the hard ground suggest a protected area.

D. Otherwise, they can be easily destroyed by currents and storms.

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ECOLOGICAL FUNCTION OF THE REEF ORGANISMS IN THE CONSTRUCTION OF HOLOCENE REEF CARBONATES OF TAIWAN

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Abstract - It is observed that the role of organisms in the construction of the reef is manifold. They may construct reef frames, either by themselves alone or in conjunction with other groups. Detailed analysis of the role of organisms in the construction of the reef carbonates, allows us to establish the ecological functions of the organisms in the construction of reef, the biological constructive processes, and the timing of reef carbonate formation.

Based on field analysis, it is observed that different processes operate to varying degrees in reef construction. These processes are mainly: **I.** Biological constructive processes, **II.** Destructive processes, **III.** Sedimentological processes, and **IV.** Diagenetic processes. This paper deals only with the ecological function of the reef organisms in the construction of reef carbonates.

1. Framework construction
Colonies attached upon one another by anchorage and accumulation through growth. The recognition of this type of reef carbonate in the field should be based on the presence of in situ framebuilders in mutual contact. The organisms of this type can be massive, branching (Fig. 1), leaf-like (Fig.2), lamellar or encrusting in form and form framestone.

An important portion of Holocene reef carbonates was formed by combining two or more different organisms (Fig.1) who show different ecological functions in reef carbonate construction. This is likely caused by the competitive intergrowth of different organisms.

2. Consolidation
Encrusting and/or cryptic encrusting organisms encrust and bind a weakly formed framework and hence consolidate them to form a rigid reef framework. In this case, these weakly constructed frameworks of different kind, once consolidated, are "wave resistant" structures even under typhoon or hurricane conditions (Figs. 1, 2 and 3).

3. Binding
Organisms could bind broken skeletons and even siliciclastic debris (in this case, it is bound by red algae) and could protect them from waves and currents to form part of a rigid reef framework (Fig.3). Otherwise, waves and currents were able to dislocate debris from the reef environment.

4. Baffling
Bafflers including skeletal, non-skeletal and poorly skeletonized organisms are seemingly very important. The non-skeletal and poorly skeletonized bafflers may be very significant, as suggested by living non-skeletal algae. They may have a very large role in the reef construction although their former presence in reef carbonates had been very difficult to recognize. Their importance must be interpreted and reconstructed from the nature of the sediments. Needless to say, in clear water condition, when there are no sediments to baffle, branching organisms do not form bafflestone (Fig.1), but instead form framestone.

5. Stabilising
Lamellar organisms cover and stabilise debris so that the debris can be rapidly cemented to form reef rocks. This type of reef carbonate can be called coverstone (Tsien, 1981, 1990, 1994).

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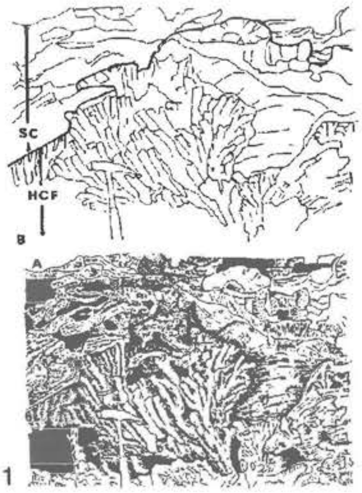

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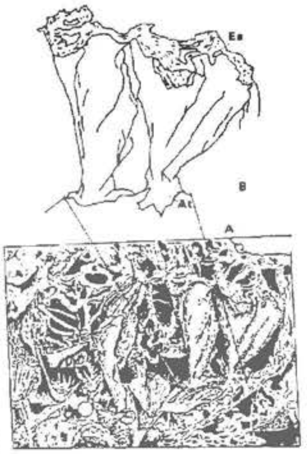

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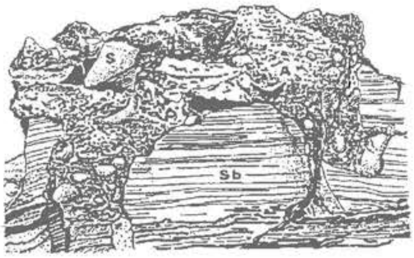

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Fig.1. **A.** Different heavily calcified branching corals which intergrew to form mutually supported open rigid frameworks which was subsequently consolidated by encrusting algae. **B.** Ecological analysis of the reef carbonate. Lower part (HCF): Reef framework formed by intergrowth of branching corals ; upper part (SC): Showing that the framework was secondarily consolidated by encrusting organisms.

Fig.2. **A.** Leaf-like corals attached upon one another to substratum by anchorage to form weakly a constructed reef framework which was subsequently consolidated by encrusting algae. **B.** Ecological analysis of the rock sample. At: Coral attached to substratum by anchorage. Ea: encrusting algae which consolidated weakly constructed framework.

Fig.3. Algae binding broken skeletons and sandy particles together to form part of a rigid reef framework. A: Algae. S: Coral fragment. Sb: Sandy particle. Thickness of the bed shown is 55cm, Chialoshui.

MESOZOIC AND CENOZOIC REEF ENVIRONMENTS

CORAL CLASTS AND REDEPOSITED CORALS AS CLUES FOR THE RECONSTRUCTION OF MESOZOIC AND TERTIARY ELEVATIONS AND DEPRESSIONS ON THE NORTH TETHYAN PASSIVE MARGIN

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Abstract - The distribution of redeposited hermatypic shallow water coral communities in base-of-slope deposits of individual basins in the Outer (Flysch) West Carpathians allows to specify the relative position of the palaeogeographic highs and depressions in the Upper Jurassic and Early Cretaceous of the North Tethyan passive margin. The distribution of the redeposited coral colonies of Upper Cretaceous and Middle Eocene age proved, that the Ždánice - Subsilesian basin was characterized by a well differentiated topography related to a system of tilted blocks formed in extensional regime. A brief characteristic of the coral reefs in the area of study is given. The palaeogeographic analysis of the distribution of coral reefs improved substantially our knowledge of the palaeotectonics in the area studied.

1. INTRODUCTION

Hermatypic shallow water coral communities are very important in the palaeogeographic reconstruction of strongly folded mountain belts. These communities, together with algae and other shallow water organisms are controlled by depth, climate and see water properties such as salinity, turbidity, supply of terrigenous clastics etc.. For these reasons we use above informations to test the palaeogeographic model of the Outer (Flysch) West Carpathians, i.e. the distribution of former topographic highs and sedimentary basins. The newly published models (MICHALÍK & SOTÁK 1990; MICHALÍK 1991) paid little attention to previous results on palaeogeographic reconstruction of the Outer West Carpathians (SLACZKA *et al.* 1976, 1984; ELIÁŠ 1979 etc.). The area of the Outer West Carpathians is strongly folded and compressed. Therefore the distribution of the coral reefs and other shallow water facies provides very important clues to reconstruct the distribution of former topographic highs in the sedimentation area.

2. GEOLOGICAL SETTING

The Outer West Carpathians - the flysch belt - form a part of the northern branch of the alpine system which is in contact with the West European Platform (European Plate). This part of the flysch belt is connected to the west with the Helveticum and the North Penninicum - the Rhenodanubian Flysch (ELIÁŠ & SCHNABEL & STRÁNÍK 1990) and to the east with the flysch belt of the North (Polish) Carpathians (POPRAWA & NEMČOK *et. al.* 1989). From a palaeogeographic point of view this area belongs to the northern part of the Tethyan domain.

The study area lies in the eastern part of the Czech Republic. The flysch belt of the Outer West Carpathians in this area consists of three groups of nappes (from below to top) - Ždánice - Subsilesian unit, Silesian unit and Magura group of units . The rocks underlying these nappes consist of the Variscan basement with the neoid cover (Upper Jurassic, Cretaceous, Paleogene) and the system of Miocene Carpathian foredeeps (SUK *et al.* 1984).

The sedimentary basins of the Outer West Carpathians developed by rifting of the Southerm margin of the West European Platform in the Jurassic. The in situ examples of the extension tectonics in the outer part of the West European Plattform were found during the oil and gas explorations in eastern Austria (SAUER *et al.* 1992). During the segmentation of the margin three main rift basins formed in the studied area (Ždánice - Subsilesian, Silesian and Magura basins). On the NW margin of the Ždánice - Subsilesian unit, on the contact with the outer part of the West European Platform, the Pavlov Carbonate Platform developed from the Oxfordian up to the Early Cretaceous. In that time of the important global eustatic transgression the sea inundated the southern rim of the West European Platform. There, from the point of view of Alpine deformations, the sedimentation area of the "Jurassic of the Bohemian Massif" developed with the Brno Carbonate Platform which remained in autochthonous position (ELIÁŠ 1981). The Brno Carbonate Platform represents a part of the girdle of carbonate platforms with small patch reefs known from western and eastern Europe (partly WILSON 1975; ELIÁŠOVÁ 1994).

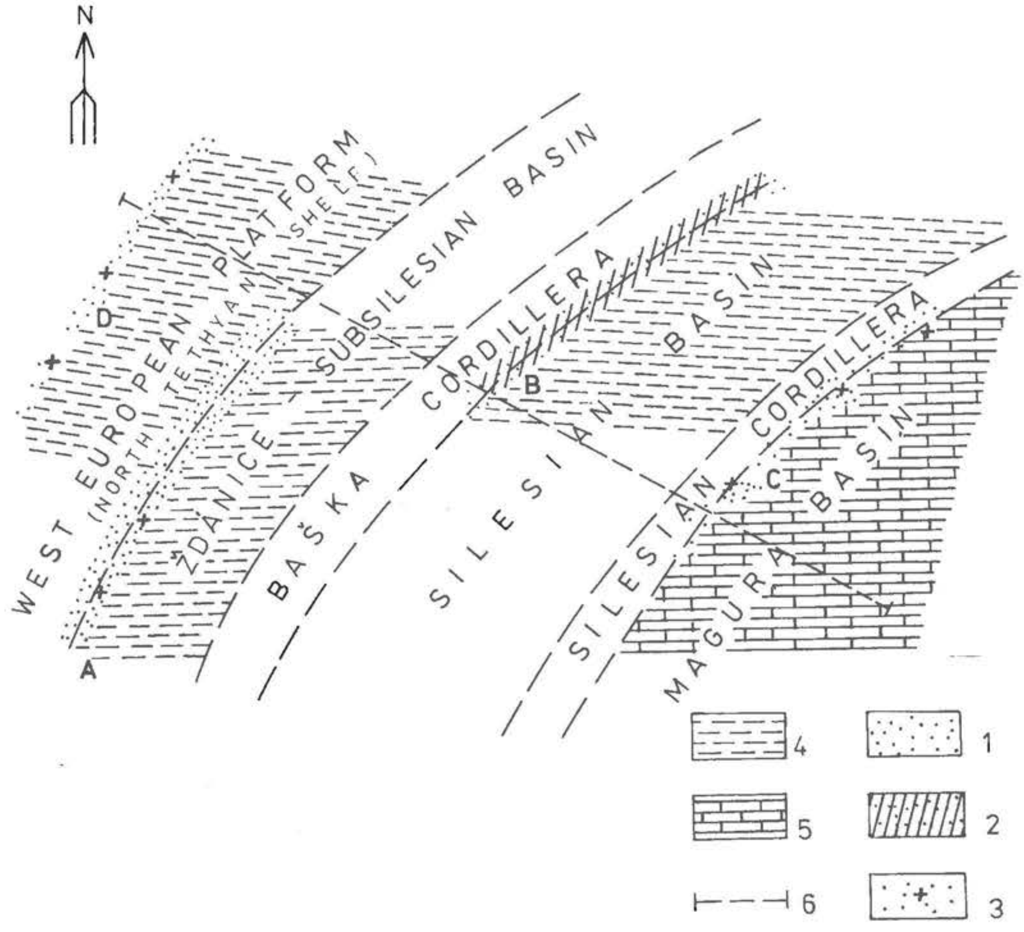


Fig. 1. Model of the distribution of the carbonate platforms and coral reefs on the North Tethyan passive margin in the Upper Jurassic and part of the Lowermost Cretaceous . The map is without scale. 1 - carbonate platform, 2 - carbonate platform and/or reef complex, 3 - patch reefs on the carbonate platform, 4 - basin facies of black-gray marls, 5 - basin facies of allodapic limestones, 6 - palaeogeographic section (fig. 2). A - Pavlov carbonate platform with patch reefs, B - Štramberk reef complex, C - carbonate platforms on the Silesian cordillera with small patch reefs.

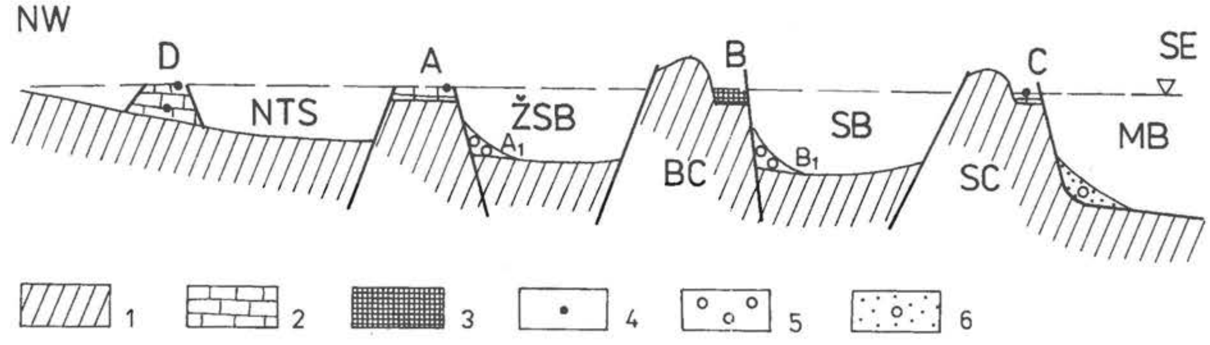


Fig. 2. Model of the North Tethyan margin in the Upper Jurassic and in the early Cretaceous. (Palaeogeographic section without scale). 1 - Fundament of the West European platform (Brunovistulicum), 2 - Carbonate platform, 3 - Carbonate platform and/or reef complex, 4 - Small patch reefs, 5 - Redeposition of clasts (partly olistoliths) in the Upper Jurassic an Early Cretaceous, 6 - Redeposition of carbonate clasts in Palaeogene (into the Soláň formation of the Magura unit). NTS - The North Tethyan shelf, ZSB - Ždánice - Subsilesian basin, B - Silesian basin, MB - Magura basin, BC - Baška cordillera, SC - Silesian cordillera, A - Pavlov carbonate platform, A1 - palaeogeographic position of the sedimentation of the Ernstbrunn Limestone, B - supposed palaeogeographic position of the reef complex - the source area of the clasts of the Štramberk limestone, B1 - palaeogeographic position of the accumulation of the clasts of the Štramberk limestone, C - supposed position of the carbonate platform with small patch reefs on the margin of the Silesian cordillera (reconstruction according to the distribution of clasts in Palaeogene sediments, D - The Brno Carbonate Platform with small patch reefs.

During the Upper Jurassic and Lower Cretaceous, the cordilleras between the sedimentary basins of the Outer West Carpathians were lined with carbonate platforms (or carbonate coastal shelves), occasionally with patch reefs. An exception represents the development of the Štramberk reef complex. It developed at the southern rim of the Baška cordillera in the Uppermost Jurassic and Lowermost Cretaceous (Standard *Calpionella* zones A and B, ELIÁŠ & ELIÁŠOVÁ 1984, 1986) from the older carbonate platform.

Latest Tithonian - Early Cretaceous represents the earliest important interval of the shallow water carbonate sedimentation with the development of reefs in the Outer West Carpathians. Beside the Štramberk reef complex, small patch reefs existed on the Brno platform, on the northern Tethys shelf, on the Pavlov Carbonate Platform and on the carbonate platform of the Silesian Cordillera.

On the Silesian Cordillera the shallow water carbonate sedimentation took place as a small carbonate platform and/or carbonate shore in contact with the Magura Basin (redeposited in the Palaeogene deposits in Chřiby Mts.) and with the Silesian Basin (redeposition in Cretaceous near Lake Roznov in Poland - MORYCOWA 1968) - Fig. 1,2.

The distribution of corals helps to reconstruct also the palaeogeography and palaeotectonics in the Upper Cretaceous and Paleogene. Extensive lenses of the bioclastic sandstones and sandy limestones with shallow water organisms (including corals) of Upper Cretaceous and Palaeogene age became known from the Ždánice

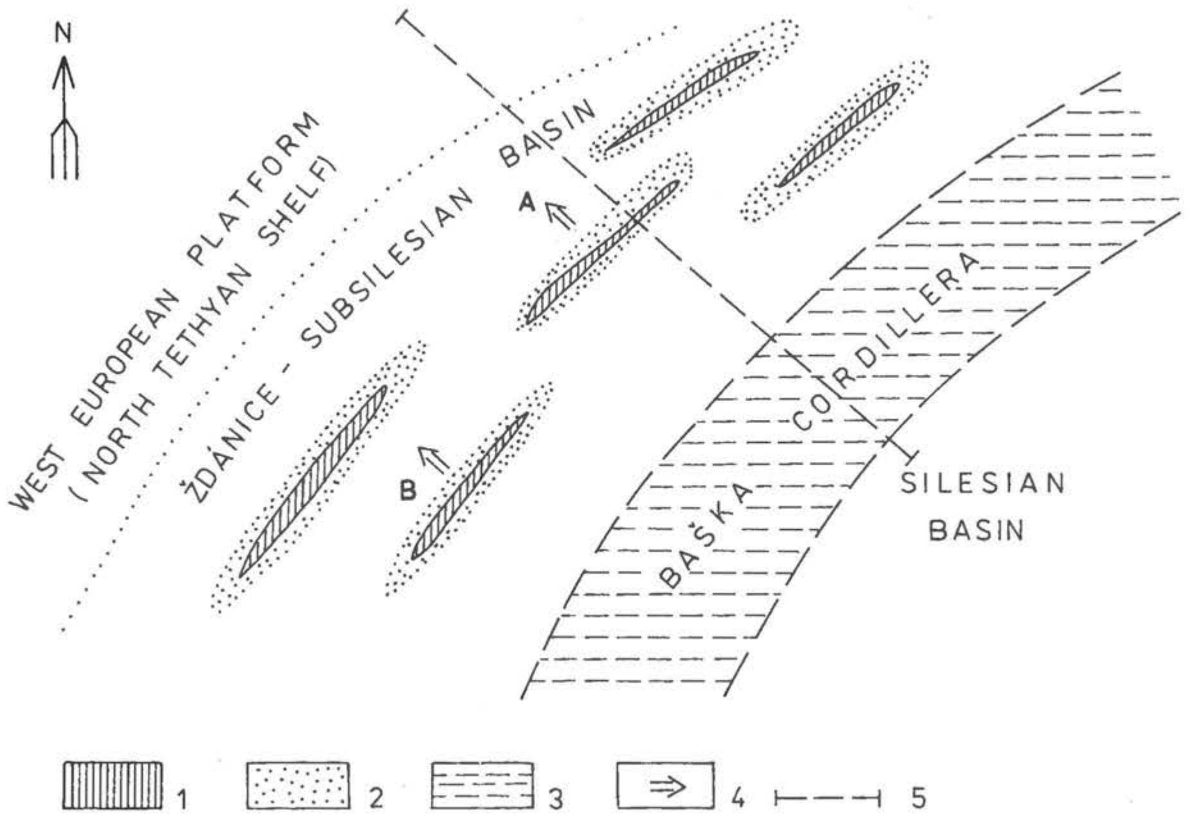


Fig 3. Model of the distribution of the facies with small coral patch reefs in the Upper Cretaceous and in the Early Palaeogene according to the supposed distribution of the elevations controlled by tilted blocks. (Palaeogeographic map without scale.) 1 - Supposed elevations on top of the tilted supracrustal blocks of the fundament (Brunovistulicum) with shallow water sedimentation (small carbonate platforms with patch reefs), 2 - Supposed palaeogeographic distribution of bodies of bioclastic sediments (bioclastic sandy limestone to sandstone with bioclastic components) - Klokočov member (Uppermost Cretaceous), Stráž facies of the Frýdlant formation (Paleocene - Middle Eocene of the Subsilesian unit) , Orbitoid sandstone (Middle Eocene) in the Submenilitic Formation (Ždánice unit) with slump bodies containing corals, 3 - Source area of clastic material (Baška cordillera), 4 - Direction of redeposition. Localities : A - Klokočov (Příbor) in the Subsilesian unit, B - Kurdějov (Hustopeče) in the Ždánice unit.

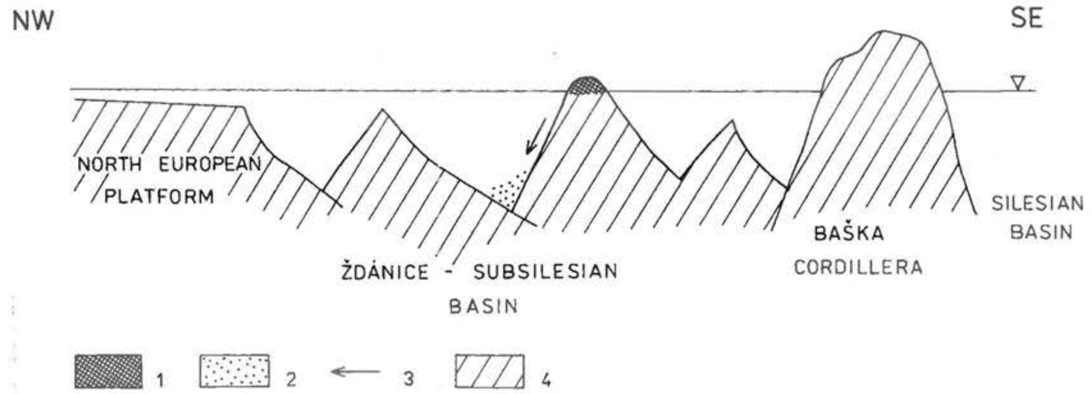
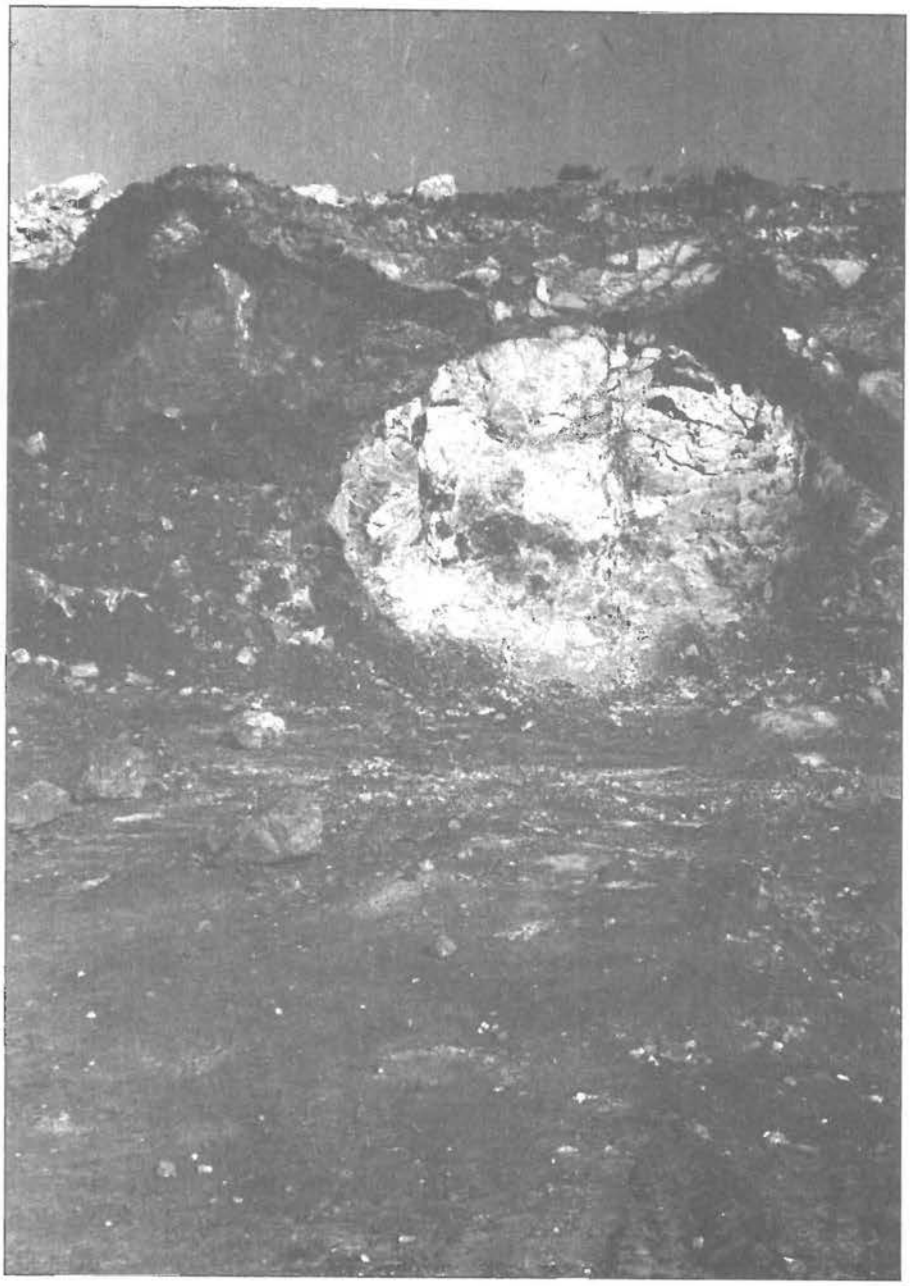


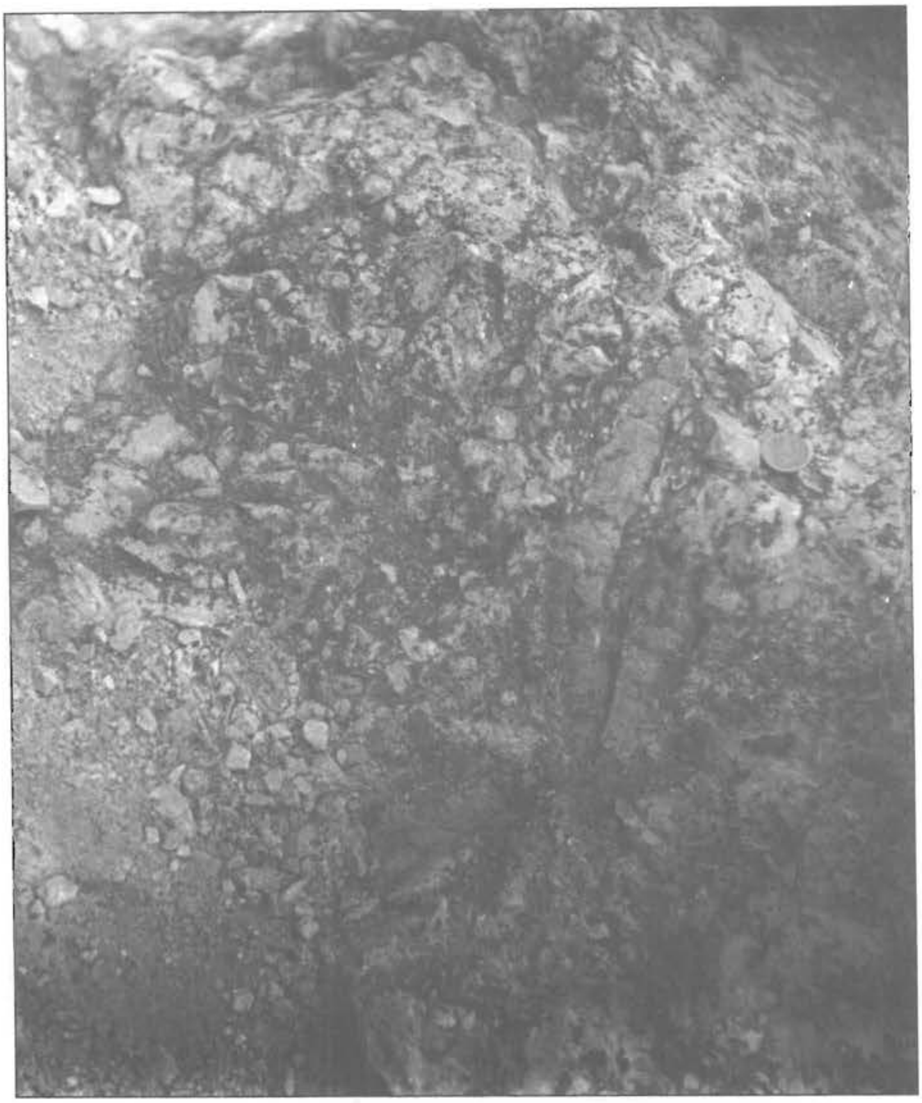
Fig 4. Model of the Ždánice - Subsilesian basin in the Upper Cretaceous and in the Early Palaeogene. (Palaeogeographic section without scale.) 1 - areas with shallow water sedimentation, with temporal patch reefs, 2 - accumulations of slumps and other redeposited sediments with corals, 3 - direction of the redeposition, 4 - basement (rifted margin of the West European platform - Brunovistulicum)

Plate 1



Great block of Štramberk limestone in the slump body of the Těšín - Hradistě formation (Early Cretaceous) from the base-of-slope facies of the Silesian Unit. Kotouč quarry. Štramberk.

Plate 2



Breccia beds of the Ernstbrunn limestone (Uppermost Jurassic - Lower Cretaceous). Base-of-slope of the Ždánice - Subsilesian unit. Svatý Kopeček. Mikulov.

- Subsilesian unit . The sedimentological analysis reveals, that these shallow water carbonate clasts derived from intrabasinal sources, i. e. tops of the tilted blocks of the basement. These tilted blocks originated from the contemporaneous extension of the basement of the Ždánice - Subsilesian Basin (Figs. 3, 4).

The system of nappes of the Outer West Carpathians developed during the final stages of the closure of the Tethys (SUK *et al.* 1984).

3. TAXONOMIC AND PALAEOGEOGRAPHIC ASPECTS

3.1. Štramberk (Silesian unit)

The Štramberk reef complex, Uppermost Jurassic - Lowermost Cretaceous in age, developed from the older (Upper Jurassic) carbonate platforms (ELIÁŠ & ELIÁŠOVÁ, 1984, 1986). We believe, that this reef complex reached its greatest extent during the stillstand of the sea-level corresponding to the global Upper Jurassic transgression maximum (pl.1).

The Štramberk reef complex is characterized by a very rich coral assemblage (ELIÁŠOVÁ 1981), of about 85 genera and numerous species. About 1/3 of the genera are endemic. From the systematic point of view the suborder Amphiastraeina ALLOITEAU 1952 dominated, with a very rich association of species and numerous individuals. Phaceloid corals are well represented.

The blocks of limestone (Štramberk Limestone) from the former reef complex and carbonate platform are embedded now in base-of-slope conglomerates and slump bodies within the Cretaceous of the Silesian unit.

3.2. Ernstbrunn limestone (Ždánice - Subsilesian unit)

The Ernstbrunn limestone developed during the Tithonian and Early Cretaceous on the talus of the Pavlov Carbonate Platform adjacent to the Ždánice - Subsilesian basin (ELIÁŠ 1992) where the corals constructed isolated patch reefs. The diversity of the corals on the Pavlov Carbonate Platform is lower than in the Stramberk reef complex (only 19 genera are recorded, ELIÁŠOVÁ 1990). All these genera and their species also are known from the Štramberk limestone. These two areas of carbonate sedimentation, which developed during the same time span, were largely connected.

Based on its stratigraphic position, age and composition (ELIÁŠ 1981; 1992), we believe that the Pavlov Carbonate Platform was also a source area of the Kobylí Limestone (the uppermost member of the Jurassic sequence of the southern part of the Bohemian Massif in eastern Austria and in the SE part of the Czech Republic).

3.3. Klokočov (near the town of Příbor, Ždánice - Subsilesian unit)

At the Klokočov locality we found 19 genera of corals (TRAUTH 1911, ELIÁŠOVÁ 1989). One species, *Actinacis remesi* Felix, 1903 is prevalent. It represents over 90 % of the individuals including big massive colonies up to 50 cm in diameter with massive growth form and irregular surface. This species probably lived in a highly stressed environment due to agitated water with suspended matter (CHEVALIER *in* GRASSÉ 1987). We suppose, that this association of corals developed as a pioneer community forming thin patches or biogenic crusts on the intrabasinal heights in the area of predominantly siliciclastic sedimentation.

The coral colonies (most probably of Cenomanian - Santonian age) were silicified before their redeposition by slumps in the Late Cretaceous (Klokočov Member of the Frýdek Formation).

3.4. Kurdějov (near the town Hustopeče, locality Holý Vrch, Ždánice - Subsilesian unit)

The geological occurrence of corals in a slump body in the Submenilitic Formation at this locality is very similar to that of Klokočov. The association of corals at the locality Holy Vrch consists of 18 genera (ELIÁŠOVÁ 1974) and was more differenciated than at Klokočov. Most of them are endemits. A relatively high number of colonies belongs to the genus *Favia* Oken, 1815 (with three species).

The geologic situation suggests that this association of corals developed in the Middle Eocene as small patch reefs or as coral carpets on intrabasinal highs (tops of the tilted blocks). The redeposition in slumps took place soon after the sedimentation. The transportation of the colonies by slumping within a rich pelitic matrix ensured the good preservation of subtle details of coral morphology.

4. CONCLUSION

The ecological and geological analysis of the coral occurrences in the Outer West Carpathians gave the good opportunity for testing the palaeogeographic and palaeotectonic reconstruction. The results confirm, that the flysch and related deposits of the Outer West Carpathians developed from the Jurassic to the Early Miocene in a system of basins rimmed by elevations (cordilleras). This system of highs and sedimentary basins developed as a result of the breakup of the southern margin of the West European Platform. The existence of these elevations is confirmed by the shallow water carbonate sedimentation (carbonate platforms partly with patch-reefs and the Štramberk reef complex). These topographic highs were source areas of carbonate clastics for the adjacent basins. The distribution of facies in the flysch basins did not change until the closing the Outer West Carpathians in the Early Miocene . According to this evolution we classify the flysch basins as a system of failed rifts (grabens), which were separated by elevations - cordilleras on the North Tethyan passive margin. The sedimentation on the Pavlov Carbonate Platform took place in the Upper Jurassic and Lower Cretaceous only. From the Upper Cretaceous we have no sedimentary records testifying its existence.

The cordilleras and the Pavlov Carbonate Platform were destroyed during the orogeny and at the closing of the sedimentary area of the Outer West Carpathians, most probably in the Carpathian and Lower Badenian (ELIÁŠ 1979; SUK *et al.* 1984, ELIÁŠ & ELIÁŠOVÁ 1984; SAUER *et al.* 1992).

The distribution of the corals confirms the existence of the intrabasinal highs in the Ždánice -Subsilesian basin also. These intrabasinal highs documented the second phase of the extension, which took place from the Upper Cretaceous up to the Middle Eocene.

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Table 1. Comparison of the reef facies in the Outer Flysch Carpathians

Locality	Pavlovské vrchy Hills	Štramberk	Silesian cordillera	Klokočov - Příbor	Kurdějov - Hustopeče
Unit	Ždánice -Subsilesian	Silesian	Magura	Ždánice - Subsilesian	Ždánice - Subsilesian
Age	Tithonian - Early Cretaceous			Lower Cenomanian	Middle Eocene
Fundament	Margin of the West European Platform	Baška cordillera	Silesian cordillera	tilted blocks in the Ždánice - Subsilesian unit	
Type of reef	patch reefs on the carbonate platform	reef complex	small patch reefs on the margin with carbonate sedimentation	relatively small reefs on local elevations	
Association of hermatypic corals	developed	very well developed	poorly (?) developed	developed	not well developed (association in stress)
Diversity of corals (genera)	19	85	?	19	18
Tectonics and subsidence	compensated subsidence			non compensated subsidence (rate of subsidence greater as biogenic sedimentation)	
Sea level	relative stillstand			interval of transgression	
Occurrence	slumps in the Uppermost Tithonian and in Cretaceous		slumps in the Palaeogene	slumps in the Late Cretaceous	slumps in the Palaeogene

SOME NEW DATA ON THE PALAEONTOLOGY AND PALAEOECOLOGY OF THE LOWER CRETACEOUS CORALS FROM THE TRANS-CASPIAN REGION

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Abstract - The Lower Cretaceous scleractinian corals are abundant in many localities which were mostly unknown up to now. They were collected from the carbonate Neocomian formations (Berriasian - Barremian) and the terrigenous middle Cretaceous ones (Barremian - Turonian). The coral fauna includes 71 species belonging to 44 genera; 3 species and 1 genus are new; 39 species haven't been found before in this area. Most of them are well known from the "Urgonian" facies. Scleractinians display four levels of renewal of their systematical composition during Berriasian - Barremian. All corals were found in the reef complexes, in which they are the most important frame-builders. Scleractinia formed bioherms, biostromes or came out to be sparse. Five types of coral preservation were distinguished by the author.

It is for the first time that the integration of the scleractinian growth forms, sizes, their internal structures and the matrix were used to discover the coral distributional patterns on that territory. As a result of this examination five types of shallow-water scleractinian settlements were established. Four of them were composed by hermatypic corals and the fifth was formed by ahermatypic Scleractinians. The influence of the different environmental characteristics such as the water turbulence, light, sedimentological regimes, periodical draining and quality of substrate on the character of the coral settlements and their occurrence were shown. Ecological succession in coral buildups was also studied. Three types of settlements would arise on the early transgression stages, the fourth occurred on the final stages of transgressions, as for the fifth it appeared when the sea level used to be stable. The facial types with the similar coral growth habits, their sizes and the same matrix were found on several levels of the Lower Cretaceous section. Such types of the cnidarian settlements are known from other Phanerozoic reef deposits. The other groups of Scleractinia, as well as Rugosa, Tabulata and Stromatoporoidea show similar patterns of distribution in reef facies.

The reef systems under study, as well as a great deal of other Lower Cretaceous reefs in the world, have developed under a stable geological regime and have rather small thicknesses. The Lower Cretaceous reefs of the Trans-Caspian region are analogous to the recent epicontinental ("monsoon") ones.

According to the composition of the Lower Cretaceous Tethys Sea corals the western part of the Central Asia basin was more closely connected with the basin of the Crimea - South Caucasus and Carpatho - Balkan region than with the seas of the Alpine region.

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CORAL FACIES FROM THE ALBIAN OF CAPE AJO (N. SPAIN)

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Abstract - The Albian section of the Cape Ajo (Cantabria) can be integrated in the Urgonian complex of the Basque-Cantabrian Basin. The section consists of 250 m of pure shallow-water carbonate platform facies punctuated by siliciclastic-rich fine-grained, clay, silt or sand intervals. Rudists and corals are the dominant macrofossils in the limestone beds, together with outsider bivalves, foraminifera, calcareous algae, brachiopods and echinoderms. Scattered coral specimens are common throughout the section although coral-rich associations only occur at specific horizons. Three of these coral-rich beds are focused in this preliminary palaeoecological and taxonomical report.

Horizon 1 consists of a 2 m thick marly interval containing abundant coral individuals and colonies in living position. The horizon 1 overlies an incipient hard-ground surface developed on top of a rudist-coral grainstone shoal facies. The marly coral facies represents a relative short pulse of deepening that is followed by a shallowing-up sequence that culminates again with a grainstone rudist shoal facies. The following taxa of plocoid meandroid and phaceloid growth forms dominate: *Columnocoenia ksiazkiewiczi* Morycowa, *Cyathophora steinmanni* Fritzsche, *Eugyra lanckoronensis* (Morycowa), *Diplogyra lamellosa eguchii* Morycowa and *Calamophylliopsis fotisalensis* (Bendukidze).

Horizon 2 contains a similar lithofacies as horizon 1: 1.5 m of marlstone with abundant coral specimens representing a pulse of deepening with respect to the underlying miliolid-rudist grainstone shoal facies. Plocoid, flabellate, trochoid, cylindrical and phaceloid coral growth forms are characteristic. The taxa determined are: *Columnocoenia ksiazkiewiczi* Morycowa, *Pentacoenia elegantula* d'Orbigny, *Pentacoenia pulchella* d'Orbigny, *Pseudocoenia slovenica* Turnšek, *Plesiophyllia acrisionae* Felix, *Acrosmilia (?) soemmanni* Fromentel, *Axosmiliopsis* sp., *Trochoidomeandra problematica* Morycowa, *Smilotrochus* sp., *Cladophyllia furcifera* Roemer and *Dendrosmilia crassa* Felix.

Horizon 3 consists of 3 m of reefal limestone forming a patch-reef buildup made up of mainly colonial corals with phaceloid, plocoid and hydnophoro-meandroid growth forms reaching individual colony sizes up to one meter embedded in a calcarenitic matrix. The analysed taxa include: *Thecosmilia dichotoma* Koby, *Cheilosmilia (?) rugosa* (Koby), *Diplogyra lamellosa eguchii* Morycowa, *Pseudocoenia slovenica* Turnšek, *Pentacoenia pulchella* d'Orbigny and *Hydnophoromeandraraea volzi* Morycowa. Horizon 1 and 2 corals suggest deposition on a lagoonal soft bottom substrate whereas horizon-3 coral facies indicate shallower-water patch-reef conditions.

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SHALLOW-MARINE LAGOONAL PATCHREEFS OF THE OXFORDIAN IN THE SWISS JURA MOUNTAINS

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Abstract - During the deposition of the Natica and Hauptmumienbank members (Vellerat Formation) and the corresponding Günsberg member and Steinibach beds (Balsthal Formation), the shallow-water carbonate sedimentation was affected by numerous terrigenous input of clays, quartz and feldspars. This is related to tectonic instabilities and relatively wet climates affecting the study area towards the end of the Middle Oxfordian and the beginning of the Late Oxfordian.

Sequence stratigraphy and cyclostratigraphy permit correlation of the different sections in detail. Analysis of the main facies components of the studied sections, clay mineralogy and palynofacies suggest wet or dry, subtropical to tropical or mediterranean climatic conditions. Lagoonal patchreefs seem to develop in well-defined time-periods corresponding to subtropical to tropical dry or wet climates with reduced influence of terrigenous input.

In lagoonal environments, patchreef buildup is dependent on factors such as depth, water turbidity, and storm frequency which in turn relate to relative sea-level, terrigenous input and seasonality, respectively. Given these conditions, lagoonal patchreefs are always at the limit of survival. In most cases a close association between corals, cyanobacteria, serpulids and/or encrusting foraminifera results in a solid bioconstruction (framestone) and gives all bioconstructors a chance to survive.

These patchreefs commonly imply different episodes of building with alternating bioconstruction and destruction by storms, suffocation by clays, invasion by shoals or sand sheets, restriction of lagoonal conditions, or emersions. Microbial encrusters, serpulids or encrusting foraminifera are less sensitive to harsh conditions and can rapidly recolonise the substrate, thus giving the corals a chance to reinstall themselves.

The development of these patchreefs is slow, as witnessed by degradation of coral surfaces and intense bioperforation by bivalves. Drastic changes in climatic conditions and/or the evolution of platform morphology - influenced by relative sea-level variations - change the environmental conditions and may lead to the demise of the patchreefs.

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REEF-BUILDING COMMUNITIES AND SEA-LEVEL CHANGES IN THE LOWER CRETACEOUS OF TURKMENISTAN

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Abstract - The Lower Cretaceous of Turkmenistan is represented by 2 major carbonate sedimentary sequences: Type I (Berriasian - Hauterivian) and Type 2 (Hauterivian-Barremian).

Most of the reef buildups are located in transgressive-system tracts (TST) and in highstand-system tracts (HST). TST reefs are better distinguished because of good preservation of coral settlements in siliciclastic and clayey sediments. HST reefs are worse to collect corals. Their assemblage of reef-builders is much more diverse and dominated by an algae-rudist-gastropod-foraminifera-echinoderm-

coral-hydrozoan-bryozoan-brachiopod community. The extensive mud facies zone is connected with a large area of reef, lagoon and a leeward reef slope. The windward slope of HST reefs has patches of normal coralgal framestone buildups and is the only site of calcareous red algae and stromatoporan growth. Reef patches are scattered among the oolite shoals. Most of HST reefs have distinct sigmoidal relief features and are ideal to study microfacies ranges. Both TST and HST reefs show recurrent extinction and rejuvenation of reef settlements. The comparison of repeated cases shows 2 general types of extinction caused by drastic environment changes: 1)-draining ; 2)- flooding. Consequently, 2 types of recolonisation are observed: 1) reef growth on a re-submerged marine-flooding surface; 2) shallowing-upward succession of a prograding reef slope.

The most often recognized "reefs" are the flat areas covered by coral settlements - "coral meadows". They occur only in transgressive semicycles of TST parasequences. They normally do not survive longer than several tens or one hundred years . The study of the surfaces of the colonies' shows a certain regularity in the succession of encrusting forms. Normally, the dead coral surface is covered by rudist or oyster bivalves and the alga(?) *Bacinella - Lithocodium*. But sometimes surfaces are coated by bryozoans, encrusting foraminifers and sponges. The first type of encruster succession is common in lower TST parasequences. The upper TST is characterized by the second type.

The shallowing upward succession of a prograding HST reef shows that an original coralgal settlement is always preceded by an infaunal bivalve community which settles in the soft siliciclastic sediment and forms a primary pavement when later colonised by corals. When carbonate accumulation reaches the minimum ebb tide sea level, the coralgal association is succeeded by a rudist-*Lithocodium*-nerineid-gastropod community with abundant large foraminifera which is covered by algal mats with numerous crustacean remains. The areal increase of the carbonate platform leads to a natural decrease of the influence of the reef framework on sedimentation in general. Often, the reef framework is largely destroyed by the subsequent erosion, and only scattered coral debris in the talus of the frontal platform indicate its former presence.

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PALAEOZOIC REEF ENVIRONMENTS

ORDOVICIAN AND SILURIAN REEFS IN THE BALTIC AREA

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Abstract - Coral, stromatoporoid and algal reefs were developed in the marginal part of the gulf-like Baltic cratonic basin in Gotland, north and central Estonia, and east to central Lithuania. They are situated at different stratigraphic levels from the middle Caradoc up to the lower Pridoli. Their appearance coincided with the transition of the Baltic Basin from an epicontinental to pericontinental phase of development, and with shifting from a temperate to the tropical climatic zone. Most of these reefs had a flat or lenticular shape, as they grew in conditions of relative tectonic and eustatic stillstand. Extensive progradation of the reef belt took place during general regression of the basin at these times. The role of stromatoporoids increased in frame building towards the end of the Silurian. Shoal-barrier type reef tracts, developed at different stratigraphic levels, were situated in the middle part of a broad carbonate shelf (platform) on the SW margin of the Baltic craton. This contrasts with Recent barrier reefs, usually located at the shelf edge of eastern margins of continents

1. INTRODUCTION

A comparatively complete sequence of Ordovician and Silurian rocks in the Baltic area shows development of reefs (carbonate buildups) over an interval of almost 40 million years, beginning in the middle Ordovician (mid-Caradoc), and ending in early Pridoli time.

Silurian reefs on the Swedish island of Gotland have been well known since first recorded by MURCHISON (1847). In the East Baltic area, reefs are less studied due to poor exposure in natural outcrops of Estonia and limited quarrying activity. Still lesser known are reefs from subsurface drill holes of the southern East Baltic, intensely studied in Lithuania by local petroleum geologists.

2. PREVIOUS STUDIES

Many papers have been published on the reefs of Gotland, recently reviewed by RIDING (1981) and by COPPER & BRUNTON (1991). The most complete list of the reef publications is found in an excursion guidebook by NEUMAN & KERSHAW (1991). In Estonia special investigations have been devoted to the reefs of the lower Wenlock (AALOE 1956, NESTOR 1990), middle Caradoc (MÄNNIL 1960; HINTS 1990), and lower Llandovery (AALOE & NESTOR 1977; NESTOR & NESTOR 1977). Additional information is available also in review papers on reefs (AALOE & EINASTO 1970, KLAAMANN & EINASTO 1982), as well as the bedrock geology of Estonia (KALJO 1970; RÔÔMUSOKS 1970). Subsurface Silurian reefs in Lithuania have been briefly treated by LAPINSKAS & CHEHAVICHIUS (1981), and LAPINSKAS (1987). A modern comprehensive summary on the Silurian geology of the Baltic Region with a detailed stratigraphic chart is included in the paper by BASSETT, KALJO & TELLER (1989).

3. GEOLOGICAL BACKGROUND

During the Ordovician and Silurian the Baltic area was part of a cratonic basin, which gradually evolved from a broad, level-bottom, shallow epicontinental sea to a bathymetrically more differentiated pericontinental sea opening south-west into the Rheic Ocean (NESTOR 1990). In the course of this process a deeper water axial depression was formed , referred to as the "Baltic Syneclise". It was characterized by argillaceous deposits (mudstones and marlstones) with planctic graptolites (see BASSETT, KALJO & TELLER 1989, Figs 119, 121 etc.). Along the margins of the

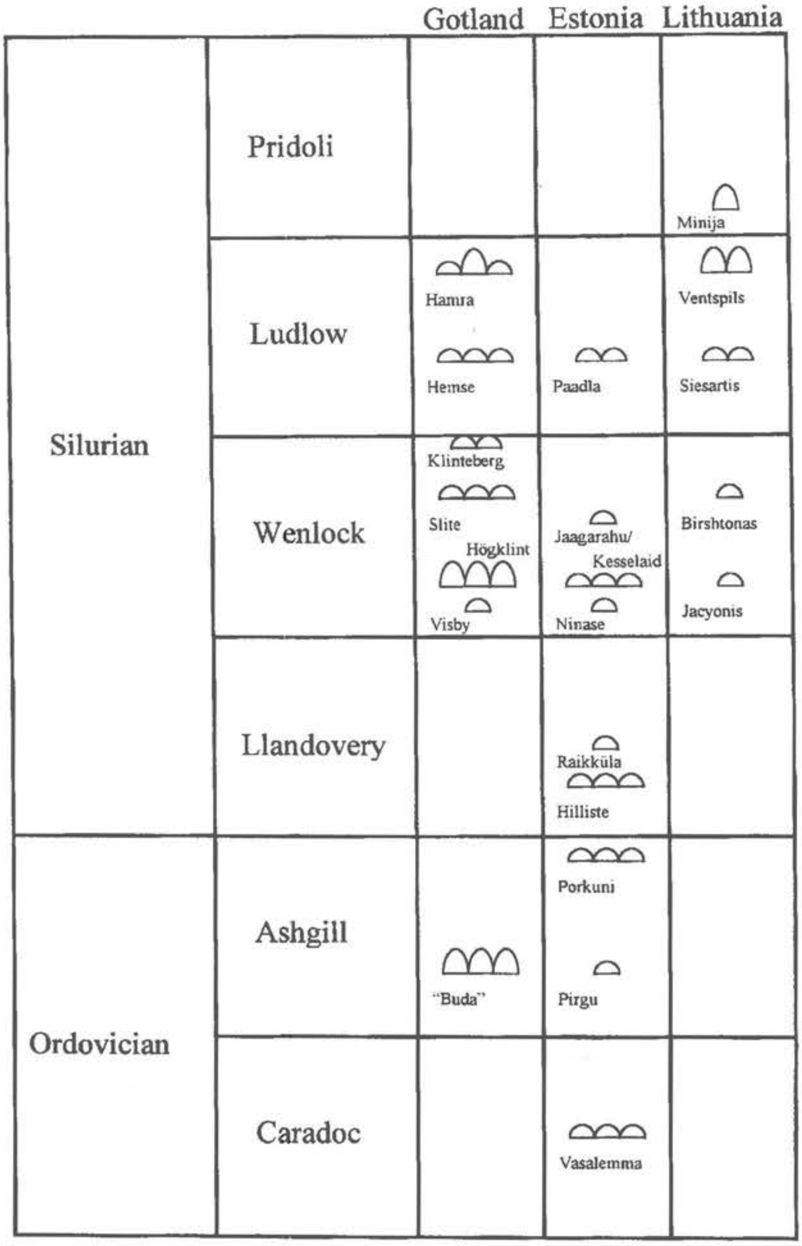

Fig.1. Stratigraphic occurrences of reefs. The size and number of signs reflects relative size and frequency of reefs in corresponding stratigraphic units.

basin, in Gotland district, north and central Estonia, and eastern Lithuania a wide belt of shallower-water carbonate sediments was developed with sporadic reefs or reef tracts. The appearance of reefs in the sequence roughly coincided with the transition from an epicontinental to pericontinental phase of basin development in Caradoc (NESTOR 1990). It also coincided with a suggested shift of the Baltica palaeocontinent from a temperate climatic zone into the tropics (see SCOTESE & McKERROW 1990, figs.8 and 9). During the late Ordovician and Silurian a generally regressive trend took place in the south-west direction, although it was cyclically interrupted by short transgressive episodes.

4. DISTRIBUTION

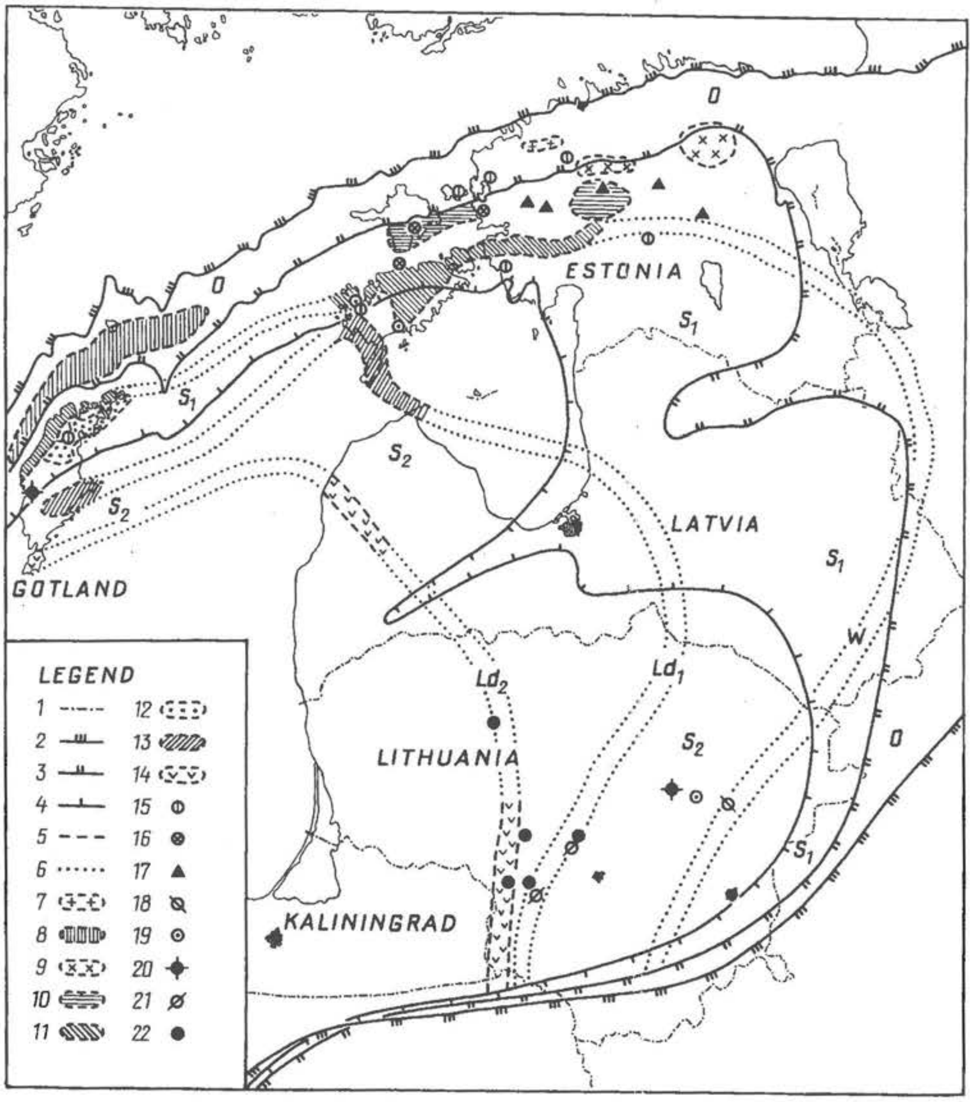

Fig.2. Distribution of reefs in the Baltic area. Legend: 1- frontier, 2- contour of the Ordovician rocks, 3- contour of the lower Silurian, 4- contour of the upper Silurian, 5- proved limit of a reef tract, 6- supposed limit; 7-14 reef areas: 7- Vasalemma, 8- "Buda", 9- Porkuni, 10- Juuru (Hilliste), 11- Högklint/ lower Jaagarahu/ Kesselaid, 12- Slite, 13- Hemse/ Paadla, 14- Hamra/ Sundre/ Ventspils; 15-22 single localities: 15- Pirgu, 16- Porkuni, 17- Raikküla, 18- Jacyonis, 19- middle Jaagarahu/ Birshtonas, 20- Klinteberg/ Siesartis, 21- Dubysa, 22-Minija.

The Baltic, Ordovician and Silurian reefs occur discontinuously at selected stratigraphic intervals from the middle Caradoc (Vasalemma Formation of the Keila and Oandu regional stages in Estonia) up to the lowermost Pridoli (Minija Formation of the Kaugatuma Stage in Lithuania) (Fig.1).In the Gotland area they occur in most of the stratigraphic units of the Wenlock and Ludlow, and also in subsurface sections of mid-Ashgill age ("Buda" carbonate mounds). The latter are also established by seismic reflection profiles below the sea-bed north of Gotland (Fig.2). In the Estonian sequence, reefs occur from the middle Caradoc up to the end of the Ludlow (Kuressaare Stage) with several interruptions in their stratigraphic succession (see KLAAMANN & EINASTO 1982). In Lithuania, reefs are well developed in the Ludlow and lower Pridoli sections in central Lithuania where they lie at a drillcore depth of 800 to 1200 m. Some records of reefs come also from the highly dolomitized Wenlockian rocks in subsurface sections of eastern Lithuania. In the deeper-water Latvian sequence reefs occur only in the upper Ludlow Ventspils Formation. At specific stratigraphic levels carbonate buildups form extensive (although, perhaps, discontinuous) belts together with related rocks, most commonly with pelmatozoan grainstones. Carbonate buildups are widespread in the middle Ashgill, where similar large carbonate mounds, consisting of micritic limestone with Stromatactis-structures, have been described from the Siljan district in central Sweden (JAANUSSON 1979), Gotland area, western and central Estonia (Fig. 2).

Lower Wenlock Högklint reefs of Gotland, mainly consisting of the stromatoporoid *Vikingia tenuis*, continue on the Estonian Island of Saaremaa in the Vilsandi Beds of the Jaagarahu Stage. These are replaced eastwards by highly dolomitized "mud-mounds" of the Kesselaid Member of the Muhu Formation (Fig. 3D). It is possible that this Wenlockian reef tract continues also in East Lithuania.

A lower Ludlow reef tract, mostly represented by stromatoporoid biostromes (KERSHAW & KEELING 1994) with *Plectostroma intermedium*, *Clathrodictyon mohicanum*, *Stromatopora bekkeri*, *Syringostromella borealis* as the main frame-builders, is traceable in the Hemse Group on Gotland, Paadla Formation on Saaremaa and in the Dubysa Formation in south-eastern Lithuania.

The upper Ludlow Hemse-Sundre reef belt of Gotland continues on Kurzeme Peninsula of Latvia and in central Lithuania as a reef complex in the Ventspils Formation (LAPINSKAS & CHEHAVICHIUS 1981), which is demonstrated by the abundance of the stromatoporoid *Plectostroma scaniense* both in the Hemse-Sundre and Ventspils reefs.

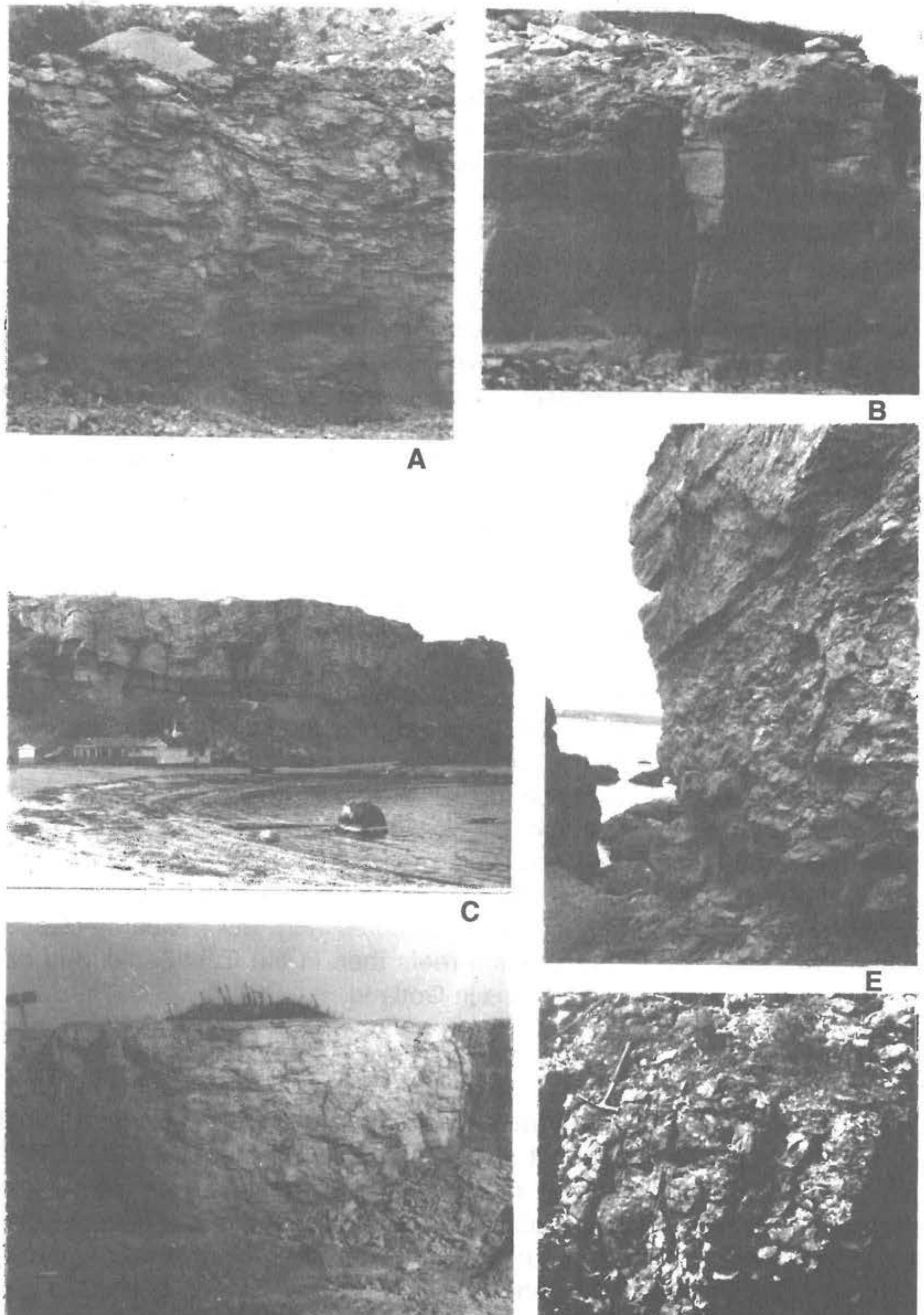

Fig.3. Examples of the early Palaeozoic carbonate buildups from the East Baltic area. A- middle Ordovician Vasalemma carbonate mound in an abandoned quarry at Vasalemma, Estonia; B- small bryozoan pioneer bioherm in pelmatozoan grainstones of the Ninase Member (lower Wenlock), Estonia, Saaremaa, Undva cliff; C- typical lenticular Högklint patch reef at Snäckgärdsbaden, Gotland; D- lower Wenlock Kesselaid "mudmound", Estonia, Muhu Island, Koguva quarry; E- lower Ludlow stromatoporoid biostrome, Hemse Group, Gotland, Kuppen; F- stromatoporoid framestone in a biostrome of the same age, Paadla Stage, Saaremaa, Riiumägi.

5. REEF MORPHOLOGY

Most commonly the Baltic early Palaeozoic reefs are represented by lenticular bodies of comparatively small sizes (thickness 1 to 10 m, horizontal diameter up to 50 m). Thickness of the largest reefs ("Buda", Högklint, Hamra, Ventspils, Minija) may reach 30 to 60 m, with diameters of 0.5 to 4 km. In the last case they appear to be coalescent biohermal agglomerates, rather than individual reef bodies. Bioherms or carbonate mounds, which developed in deeper-water argillaceous sediments below wave base ("Buda" mounds, Upper-Visby bioherms) may be about as thick as wide, or their thickness may exceed their diameter. More common are flat lenticular bodies, which developed in a high energy, shallow water environment whose end member is a biostrome (Fig.3E). In some cases a reef developed as a small pioneer bioherm and, growing into the turbulent zone, expanded sidewards rapidly, becoming a biostromal unit in its upper part (RIDING & WATTS 1991). The prevailingly flat shape of the reefs suggests that they developed during a relative stillstand of sea-level (Fig.3C). In general, flat reefs were elevated only a few metres above the surrounding sea floor. A higher slope may be expected for upper Ordovician "Buda" mounds, and for the upper Silurian Ventspils and Minija stromatoporoid reefs of the south East-Baltic area, developed in a deeper-water environment on the outer shelf.

In most cases, massive reef cores were surrounded by flanking bioclastic limestones, prevailingly as pelmatozoan grain- and rudstones. Flanking rocks of the Högklint reefs contain an abundant pelletal component, especially in topmost parts (JAANUSSON, pers. comm.). The Lower Wenlock Kesselaid "mudmounds" of Estonia are enclosed by dolomitized, slightly kerogenous, argillaceous flagstones of probably restricted shelf or lagoonal origin (NESTOR 1990). Dips of the flanking beds may vary from almost horizontal to very irregular due to penecontemporaneously depressed strata underneath the reef cores (Fig. 3D). Coarse-clastic reef talus is better developed in the Gotland reefs than in the East-Baltic, and can be explained by more open-sea conditions in Gotland.

6. FRAME BUILDERS

The earliest, Ordovician buildups (Vasalemma and Buda mounds) consist mostly of micritic carbonate material without a visible skeletal frame (JAANUSSON 1979, HINTS 1990). Scattered skeletal remains of bryozoans, algae, pelmatozoans, corals, etc. occur in rather small quantities. Stromatoporoids are absent. The topmost Ordovician and lowermost Silurian (Hirnantian - Aeronian) small bioherms and biostromes in the Porkuni, Juuru and Raikküla regional stages of Estonia show a rather diverse assemblage of frame builders. These include tabulate and rugose corals, stromatoporoids, algae, cyanobacteria, bryozoans with slight predominance of tabulates (AALOE & NESTOR 1977; NESTOR & NESTOR 1977). In the Wenlock and Ludlow reefs, stromatoporoids gained dominance, particularly in the shallowest water biostromes (Fig. 3E-F). However, in deeper water (>10m) bioherms corals still prevailed. In the lower Wenlock of Estonia, small bryozoan bioherms have been described in the Ninase Member of the Jaani Formation (Fig.3B; AALOE & EINASTO 1970), and frameless dolomitized Kesselaid "mudmounds" (Fig.3D), laterally replacing Högklint-Jaagarahu coral-stromatoporoid reefs in eastern, more restricted marine sections of Estonia. Summing up, the increasing importance of stromatoporoids in frame-building was the most remarkable trend in the evolution of the reefs in the Baltic area. It was combined with a decrease in the diversity of frame-builders.

7. GENERAL ENVIRONMENTAL SETTINGS

A facies model worked out for the Baltic Silurian Basin (NESTOR & EINASTO 1977, NESTOR 1990) demonstrates that in most cases coral-stromatoporoid reefs and related rocks formed low shoal or barrier complexes in the high-energy middle part of a broad carbonate shelf (platform), being replaced in the offshore direction by biomicritic limestones of the open or outer shelf and shorewards by lagoonal or restricted-shelf dolomicritic rocks. Only lower Wenlock Kesselaid reefs in Estonia had a more shoreward position, whereas "Buda", Visby, Ventspils and Minija reefs were located seawards, nearer to the outer edge of the carbonate platform (Fig.4). The sea floor gradient, and correspondingly the width of the carbonate platform and facies belts, was different for different sectors of the Baltic Basin. Apparently, it was somewhat steeper in the Gotland area and extremely gently sloping in Estonia. This is indirectly demonstrated by the extent of the gradual progradation of the reef belt, which was about 200 km for Estonia and less than 100 km for Gotland (Fig.2). It also means that more open sea conditions, favourable for reef development, prevailed in the Gotland area.

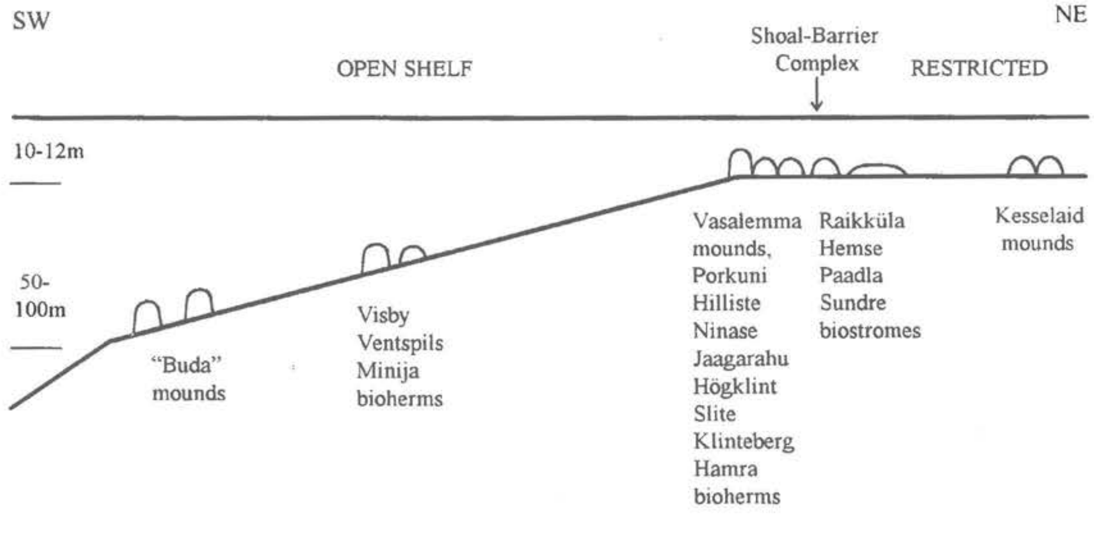

Fig.4. Main environmental settings of the Baltic early Palaeozoic reefs.

Judging from the gradual shifting of the reef tract, it becomes evident that no strong tectonic control of the reef development existed. Limited thickness of the individual reefs and reef complexes, often characterized by a shallowing up sequence (RIDING & WATTS 1991), as well as by extensive progradation of the reef tract, shows that reefs developed under the conditions of a general regression of the Baltic Basin, from time to time interrupted by short-living deepening events.

The Baltic Early Palaeozoic reefs, although forming extensive shoal-barrier complexes, developed in a different tectonic setting than the Great Barrier Reef of Australia, situated along the continental margin exposed to the trade currents. According to the most recent reconstructions (*e.g.* SCOTESE & McKERROW 1990), the Baltic Basin was located at the south-western margin of the Baltica Continent and reefs developed far away from the tectonic continental margin (Tornquist-Teisseyre Lineament). However, there are rather similar conditions for reef formation in the Gulf of Mexico.

8. CONCLUSIONS

The appearance of reefs in the Baltic area in the middle Caradoc coincided with the transition of the Baltic Basin from an epicontinental to the pericontinental phase of development, and with shift from temperate to tropical latitudes. A flat lenticular shape of many reefs suggests their development in the conditions of relative tectonic and eustatic stillstand. Extensive progradation of the reef belt took place due to general regression of the basin. The role of stromatoporoids increased in framebuilding towards the end of the Silurian. Reefs were generally situated in the middle part of the broad carbonate shelf (platform) far away from the tectonical margin of the Baltica Continent.

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PRELIMINARY SEDIMENTOLOGICAL STUDY OF AN EARLY FRASNIAN BUILDUP IN THE HOLY CROSS MTS., CENTRAL POLAND.

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Abstract - The studied area is situated in the Kowala quarry (near the Kowala vicinity) at the southern limb of the Galezice syncline (Kielce region, southern Holy Cross Mts., Central Poland). In the eastern wall of the quarry, a small bioherm is exposed and approximately corresponds in age to the middle part of the *Polygnathus asymmetricus* zone (Kadzielnia Member - Kowala Formation), (SZULCZEWSKI & RACKI 1981; RACKI 1992). This small bioherm (only 4 meters in thickness) is embedded within stratified biostromal limestones and consists of a massive, lenticular and unbedded body of light grey to grey-rose limestones. Its upper surface displays a low relief but the buildups are known as peculiar habitats marked by distinctive diverse biota (SZULCZEWSKI & RACKI 1981; RACKI 1992).

The sedimentological analysis of the bioherm and its surrounding beds is based on the definition of three major microfacies: the build-up is composed of micritic boundstones - or coverstones (TSIEN/ 1981) -, with sheet-like stromatoporoids in growth position, corals (*Alveolites*, stromatactoid structures, sometimes with red internal sediment and also of packstones rich in brachiopods, echinoderms and coarse coral fragments. These packstones could result from storm wave action, responsible for episodic destructions of the build-up. We suggest that the bioherm grew between normal wave base and storm wave base, and probably in the photic zone (presence of dasycladaceans). Packstones and grainstones constitute the embedding biostromal beds, rich in fragments of stromatoporoids, corals, brachiopods, echinoderms and peloids. Mixed with this open-marine fauna, many calcispheres indicate the influence of a relatively nearby back-reef system. The sediments display multiple encrustations and reworking. These features indicate that deposition could have occurred within or above normal wave base. Finally, more argillaceous bioturbated wackestones and packstones overly this succession. The benthic and hemi-pelagic fauna is scarce but the calcispheres are still present and point to the persistence of the more restricted areas. This level (*Phlogoiderhynchus* Marly Level) corresponds to a widespread marine flooding event and to the period of the maximum water depth (RACKI 1992). below the normal wave base and photic zone but, at Kowala, probably within the storm wave base.

The succession and the shifts of the microfacies indicate that the relative sea-level fluctuations are apparently well recorded and that deposition could have occurred on a gently inclined carbonate ramp (SZULCZEWSKI & RACKI 1981). In this hypothesis, the bioherm would be established in the mid- ramp zone, at a depth of approximately 40 meters, in the photic zone and below the normal wave base.

According to ZIEGLER's (1990) palaeogeographic reconstructions, the Polish Frasnian carbonate shelf belonged to an extensive back-arc rift system. In such a system, the previously suggested carbonate ramp could develop on the gentle slope of faulted or tilted blocks. The presence of a probably discontinuous stromatoporoid-coral barrier reef, situated on the top of the shallower blocks, could explain the persistence of a back reef system and its influence on the ramp sedimentation. In this context, the destruction of the barrier reef would be the origin of the detrital limestones ("Detrital Stromatoporoids Beds") which constitute the flanking facies of distinctly larger grey mud mounds (above 50 meters thick), visible at Kielce (Kadzielnia Quarry). But the exact relations between these mounds and their flanking facies are still to specify.
We suggest that this kind of mud mound could have grown at the foot of the relatively abrupt "reefside" of the blocks (study in progress).

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MONTICULES MICRITIQUES FRASNIENS DE LA BELGIQUE

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Abstract - Au cours du Frasnien, plusieurs épisodes de développement de monticules micritiques se succèdent dans la partie méridionale de l' actuel Synclinorium de Dinant. Suivant le contexte eustatique, ces édifices croissent au large d'une plate-forme barrée (Membre du Lion, partie moyenne du Frasnien) ou sur une rampe homoclinale (Membre de l'Arche, partie inférieure du Frasnien et Formation de Neuville, partie supérieure du Frasnien). Un modèle des bioconstructions de la Formation de Neuville a été développé (BOULVAIN 1993; BOURQUE & BOULVAIN 1993). Il s'agit de lentilles calcaires de 50 à 80 m de puissance, isolées au sein d'un encaissant argileux. Bien que les coraux ne soient pas les organismes constructeurs principaux, l'utilisation de trois cénozones à rugueux permet une stratigraphie fine des édifices et de leur encaissant (COEN-AUBERT 1982). Brièvement, de la base au sommet des monticules, on observe la séquence suivante:

- surmontant les calcaires argileux infra- et péri-biohermaux, des mudstones rouges à stromatactis et spicules d'éponges (MF3);
- ces sédiments s'enrichissent progressivement d'abord en coraux et crinoïdes (MF4), ensuite en stromatopores, péloïdes algaires et *Sphaerocodium* (MF5); des wackestones roses à *fenestrae*, brachiopodes, péloïdes, coraux (MF6) soulignent des augmentations périodiques de la turbulence;
- vers le coeur des biohermes apparaissent des bindstones algaires et cryptalgaires gris à coraux, stromatopores et *Renalcis* (MF8) et des packstones à péloïdes et Codiacées-Udotéacées (MF8), tandis qu'en périphérie s'observe une forte extension des faciès rouges à coraux, crinoïdes, péloïdes (MF5) qui progradent sur les sédiments argileux péri-biohermaux entremêlés de coulées crinoïdiques (MF9);
- l'extrême sommet des monticules est caractérisé par une récurrence rapide des faciès rouges à coraux (MF4), puis à stromatactis (MF3), précédant l'envahissement par des schistes à faune appauvrie.

Ces monticules se sont développés d'abord sous la zone d'action des vagues et sous la zone photique, en milieu micro-aérophile permettant le développement des bactéries ferro-oxydantes à l'origine du pigment hématitique (MF3-4). Le régime est transgressif et le taux d'accrétion des monticules est légèrement supérieur à l'élévation relative du niveau marin. La zone d'action des vagues de tempête et la zone photique des algues bleu-vertes sont atteintes avec le développement des faciès à péloïdes (MF5-6). Les faciès algaires et cryptalgaires gris (MF7-8) se développent dans la zone d'action des vagues normales, en milieu bien oxygéné (disparition des bactéries ferro-oxydantes) tandis que progradent sur les flancs des édifices, des faciès plus riches en coraux (MF5), le tout à la faveur

d'une baisse eustatique à l 'échelle du bassin. La récurrence des faciès rouges est due à un retour au régime transgressif avec une élévation du niveau marin plus rapide que le taux d'accrétion biohermal.

Les monticules du Membre de l'Arche présentent une succession de faciès plus simple, débutant directement avec des faciès roses à coraux, stromatopores, crinoïdes, péloïdes (MF5) et se poursuivant ensuite par des calcaires gris algaires et cryptalgaires (MF7-8). Ceci implique une profondeur initiale de développement moindre que dans le cas des biohermes de la Formation de Neuville.

Ces observations, basées sur la succession des faciès biohermaux et sur la géométrie de leurs surfaces de transition, sont confirmées par l'étude de coupes corrélées stratigraphiquement, situées en milieu non biohermal, au nord du bassin de sédimentation (BOULVAIN & COEN-AUBERT 1989).

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CORAL KNOLLS, THICKETS AND MICRO-MUDMOUNDS IN THE EARLYSILURIAN JUPITER FORMATION (LLANDOVERY), ANTICOSTI ISLAND, E CANADA

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Abstract - Patch reefs are developed at four different levels within the ~800m thick Ashgill-Llandovery, equatorial, carbonate platform succession of Anticosti island. Reefs occur within the Rawtheyan, Hirnantian (directly below the Ordovician-Silurian boundary), Aeronian and Telychian stages, probably in response to global climatic and sealevel changes stimulated by late Ordovician glaciation and transgressive-regressive events following deglaciation in the southern hemisphere. Here, only the small coral knolls and thickets, and micro- mudmounds of the East Point Member, Jupiter Formation (Aeronian) are treated. The East Point patch reefs are up to 4m in thickness, with maximal diameters of <10m. Climax stages of these small reefs are dominated by *Paleofavosites, Catenipora* or small syringoporid tabulates, or by phaceloid rugosans such as entelophyllids or the thamnastreoid genus *Palaearaea*, previously known only from Siberia. Stromatoporoid sponges, calcareous algae and crinoids are rare, but brachiopods are common within the coral thickets. Reef cores, the pioneering stages of these patch reefs, consist of 'micro- mudmounds' which may weather out in toto, and consist of micrites bound by crinoid holdfasts, featuring beautifully preserved stromatactid structures. The reef cores may be as little as 50cm thick and <50 cm in diameter, being

almost concretionary in nature, suggesting that such micro-mudmounds may form in relief at a very early stage of patch reef development. These appear to be some of the smallest mud-mounds recorded in the geologic record. The East Point patch reefs appear to have been terminated rapidly during a transgressive, deepening phase on the Anticosti platform, being succeeded by shales carrying dense brachiopod concentrations, with only rare small hemispherical favositid corals present.

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DEVONIAN SHALLOW MARINE ENVIRONMENTS OF THE GRAZ PALAEOZOIC AFFECTED BY RIFTING

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Abstract - The "Graz Palaeozoic" (GP), represents a terrain of unknown style. It was separated and removed from Pangaea, and it is found today as a pile of nappes resting on metamorphic basement: all present contacts of this thrust complex are tectonic ones. The root zones of the nappes are not known.

The nappe pile comprises the following three major thrust sheets from bottom to top, differing in sedimentary facies, stratigraphic range and metamorphic overprint:
The lower nappe system comprises the 'Schöckl-Group', 'Passail-Group' and 'Anger Crystalline Complex'. Besides the common Alpine (Early to Late Cretaceous) deformation of the GP in this basal nappe system minor Variscan deformation under upper greenschist facies conditions (locally Amphibolite facies) is detected. The intermediate nappe system includes the 'Laufnitzdorf-Group' and the 'Kalkschiefer-Group'. Both nappe groups occur in different structural levels. The upper nappe system comprises the 'Rannach- and Hochlantsch-Group' and is of special interest for the following considerations. The Palaeozoic nappe pile is unconformly overlain by the Kainach Gosau, a sequence starting with conglomerates including local detritus and locally dominating Mesozoic pebbles indicating a short transport.

Studying the development of the Graz Palaeozoic raises the following questions :
* To what extent did the terrain obtain its "Variscan" status from large scale plate tectonic events, still being part of an older plate?
* What was the effect of an older deformation phase, before it became effected by Alpidic orogenesis?

Microfacial investigations, sedimentological, palaeoecological and palaeomagnetic data indicate that the Graz Palaeozoic was part of a carbonate platform geographically located at the northern shelf areas of Gondwana, which has continuously drifted northward into subtropical to tropical areas. Persistent subsidence in the uppermost nappe system is documented by progressive carbonate production from Silurian to Upper Devonian. Interaction of a favourable palaeolatitude and the specific configuration of the basin is expressed by strata rich in macrofauna from Emsian to Frasnian. Looking at the evolution of the entire Palaeozoic of Graz there is a general trend to greater waterdepth in time. Overall deepening is explained by the development of graben structures, beginning in the Silurian. The N-S-oriented subsiding axis of the basin is connected with the poles of hyperthermal anomalies (*e.g.* Silurian volcanoes). Hyperthermies are linked with subsequent subsidence in space and time. Increasing thickness of formations from north to south agrees with this interpretation.
The thermal history of this area has been investigated on a large number of outcrop samples by

means of vitrinite reflectance measurements, illite crystallinity including clay mineralogy studies and conodont colour alteration index: Average values of 9.9 % VR_{max}, 0.19° $\Delta 2\upsilon$ CAI 5.5 for the lower nappe system record epizonal metamorphic conditions. The Laufnitzdorf-Group shows anchizonal conditions (6.4 % VR_{max}, 0.28° $\Delta 2\upsilon$, CAI 5). The Kalkschiefer-Group suffered epizonal metamorphic conditions (9.9 % VR_{max}, 0.21° $\Delta 2\upsilon$, CAI 5.5) whereas the Rannach-and Hochlantsch-Group show an anchizonal metamorphic overprint (5.4 % VR_{max}, 0.27° $\Delta 2J\upsilon$, CAI 5).

There is evidence of metamorphic gaps between nappes and in some areas epizonal nappes overlie anchizonal ones. This indicates the preservation of preorogene thermal conditions. Illite crystallinity - vitrinite reflectance correlation, the coalification-maxima of the Siluro-Devonian volcanic centers as well as the chemical characteristics of the alkaline mafic volcanoclastics are hints for a long lasting initial rift system. Very high heatflow with calculated temperatures about 300° C for the Rannach-Hochlantsch-Group is also recorded by additional fluid-inclusion studies of authigenic quartz crystals. Few reliable radiometric data show evidence for Late Palaeozoic cooling.

We have reconstructed the upper nappe system by a stepwise taking back of the Alpidic nappe movement. This reconstruction shows a perfect fitting of all pieces of the tectonic puzzle. In the reestablished nappe outcrops of the 'Barrandei-Limestone', a formation developed in the Rannach- and Hochlantsch-nappe, are forming an arc surrounding the two volcanic centers. This arc of back-reef sediments marks the margin of a Middle to Upper Devonian carbonate platform created by rifting. Four megacycles of "reefal deposits" showing a progressive evolution —starting with semilagoonal environments with pioneer benthic communities and ending with coral-stromatoporoid bioherms— may be distinguished. However, these megacycles themselves can be divided into cycles of minor importance concerning their internal trends in development. All megacycles are independent; they are restricted only to certain lithostratigraphic units. That means: changes of megacycles are apparent in changes of lithotypes.

First Megacycle: Emsian *Amphipora*-Mounds

The 'Dolomitsandstein-Fm.', a peritidal succession, follows the basal volcanoclastic sediments. This succession starts perhaps at lower Pragian and consists of two different members separated by volcanoclastics. The lower member is interpreted as sand bars, whereas the upper member which is (lower?) Emsian in time contains meadows of *Amphipora ramosa desquamata*. Looking over the typical mound-shaped bodies of the latter, the huge number of individuals and the lack of disarticulated coenostea the *Amphipora*-beds are interpreted as wave-resistant bioconstructions.

Second Megacycle: Eifelian Coral-Stromatoporoid-Biostrome

Overlying or interfingering the 'Dolomitsandstein-Fm.' the 'Barrandei-Limestone' is developed. Predominance of typical "reefbuilding organisms" is conspicuous in all sections. But even so, there is no evidence in the field for a "true reef".

The megacycle is finished by a repetition of tidal flat deposits similar to those of the 'Dolomitsandstein-Fm.' and was presumably caused by an eustatic sea level rise.

Third Megacycle: Givetian Biostrome/Patch Reefs

Transgression resulted in the formation of sequences which show sharp lithofacial/biofacial contrasts: In both upper nappes there are mudstones as well as small patch reefs or biostromal deposits. These developments are variable due to local environmental constraints and therefore different lithostratigraphic terms exist. In the 'Kanzel-Limestone' small *Amphipora*-mounds followed by beds with scattered chaetetids, *Favosites, Thamnopora, Thamnophyllum*, etc. In a transitional zone between Rannach- and Hochlantsch-Group a succession consisting of *Amphipora*-beds, microbolite mounds and cnidarian patch-reefs with *Stachyodes, Heliolites, Favosites, Alveolites,* thamnoporids, disk shaped stromatoporoids and solitary rugose corals are developed. Biostromal bodies constructed by the organisms mentioned above occur in the 'Tyrnaueralm-Fm.' (Hochlantsch-Group).

Fourth Megacycle:
Upper Givetian to (?)Frasnian "*Hexagonaria*"-Bioherms
Restricted only to the Hochlantsch group the last bioconstructions are developed. The 'Zachenspitz-Fm.' represents a succession of several basal *Amphipora*-beds alternating in biohermal "Hexagonarian"-Alveolitid-Stromatoporoid baffle- to boundstones. (Micro)Facial investigations indicate a shallow offshore depositional environment with pelagic fauna in the inter-bioherm-facies.

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MIDDLE DEVONIAN REEF-INITIAL FACIES FROM THE RHENISH SCHIEFERGEBIRGE (SAUERLAND AND EIFEL), WESTERN GERMANY

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Abstract - Based on faunal, floral, macro- and microfacies analysis of 4 Middle Devonian (latest Eifelian/early Givetian) limestone sections in the Sauerland (Messinghausen and Brilon quarry = Mes. anticline and Bri. syncline and Steltenberg quarry = Remscheid-Altenaer anticline) and Eifel, (Dreimühlenwald/Korea quarry = Hillesheim syncline), the ecological successions : Colonisation, Diversification -Domination are described and interpreted.

The palaeogeographic setting of the 4 localities is very different: Messinghausen represents a protected forereef region on the shelf margin which was punctuated by vulcanoclastic seamounts and Brilon a more open shelf margin region. Steltenberg represents a protected to sublagoon region of the inner shelf and Dreimühlenwald/Korea a protected shelf region behind a high area.

The quality of microfacial data is tested by multivariate statistical methods.

The universal results of the ecological successions are:
For an initial colonization the species needed shallow water conditions (Indicators: *Sycidium, Coelotrochium, Girvanella* and chlorophytes).

Other important control factors are:
a) Abiotic environmental factors: sedimentation conditions, bathymetry conditions, substratum and water energy.
b) Biotic factors: spatial competition and interaction of organism. If the abiotic factors are too unfriendly for the organism—for example high clastic sedimentation rate or high water energy—only local initial pioneer biocoenoses could develop (Brilon, Dreimühlenwald/Korea quarry). For example, stromatoporoids, tabulate and rugose corals, brachiopods and crinoids.

On the other hand, ideal environmental conditions lead to (sections of Messinghausen and Steltenberg) a three-stage sequence with spatial competition and/or interaction of organisms: Colonisation (2-4 cm thick), diversification (10-20 cm thick) and domination (55 cm thick). The successions reach together thicknesses of about 72 cm in the vertical sections.

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MIDDLE DEVONIAN *Pseudopalaeoporella lummatonensis* (GREEN ALGA) BIOTOPES OF THE RHENISH SCHIEFERGEBIRGE (EIFEL AND SAUERLAND), WESTERN GERMANY

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Abstract - *Pseudopalaeoporella lummatonensis* is an udoteacean green alga known only from Middle Devonian carbonates in Europe: as far as Spain and as far east as the Ural Mountains. Recent discoveries of *Pseudopalaeoporella* in the Eifel and Sauerland of Western Germany have yielded finely preserved specimens of different marine biotopes. Based on faunal, floral, macro- and microfacies analyses, the following fossil reef communities and reef constructions can be reconstructed:

1. *Pseudopalaeoporella* biostrome meadows

a) Locality and age: Messinghausen quarry from the Messinghausen anticline in the Sauerland (early Givetian); Rauhheck & Dockel quarries from the western Hillesheim syncline in the Eifel (Rech Member / early Givetian) and Korea & Dreimühlenwald quarries from the eastern Hillesheim syncline (Eowotan/ earliest Givetian) and Ko-Hill (syncline with Ley Member/Givetian) from the western Hillesheim syncline in the Eifel.

b) Facies and microfacies: green biomicrite (floatstone/bafflestone) with bentonite (Messinghausen); microbioclastic wackestone/bafflestone/floatstone ("Fettkalk"= limestone of "greasy"appearance) of Rauhheck & Dockel; grey limey marl beds with marly-silty parts (wackestone/bafflestone/floatstone) of Korea & Dreimühlenwald and micrite carbonate and micropeloidal floatstone of the Ko-Hill.

c) The same fauna of the different facies: brachiopods, rugose corals, sponge spicules, foraminifera and *Belodella* (conodont).

d) Palaeoenvironment: all localities can be interpreted as a very shallow and protected region of the subtidal zone.

2. Mud mounds ? with *Pseudopalaeoporella*

a) Locality and age: Weinberg quarries (latest Eifelian, Ahbach Formation, Maiweiler Subformation) and Rauhheck quarry (Wotan Member) of the western Hillesheim syncline (Eifel).

b) Facies and microfacies: red to grey biomicrites (mudstones and wackestones) with stromatactis fabrics. These biomicrites form mounds up to 20m high and down to 1km in diameter.

c) Associated fauna and flora: *Girvanella* (cyanobacteria), calcisponges (spicules), fenestellid bryozoans, echinoids, crinoids, ostracods, foraminifera, polygnathids/ *Belodella* (conodonts) and *Stachyodes* (branched stromatoporoid). Globular stromatoporoids and tabulate corals are arranged (all 1m or more in the vertical profile) in a patch reef-like manner.

d) Palaeoenvironment: protected with influence of the open marine region of the shallow subtidal zone.

3. Frame-builders with *Pseudopalaeoporella* (biostrom bioherm)

a) Locality and age: Steltenberg quarry from the Remscheid-Altenaer anticline in the Sauerland ("Schwelm" facies/earliest Givetian); Rauhheck & Dockel quarries (Wotan and Rech Member/early Givetian) and also Korea & Dreimühlen quarries from the eastern Hillesheimer syncline (Wotan Member / early Givetian).

b) Facies and microfacies: dark cyclical sequence of biomicrite (wackestones/packstones) of the Steltenberg; biomicrite and sparry carbonate (packstone/grainstone) of the Rauhheck & Dockel and calcarenite/microbioclastic peloid grainstones (packstones) of Korea & Dockel.

c) The same fauna and flora of the different facies: stromatoporoids, foraminifera, calcisponges (spicules), chlorophytes, *Girvanella*, rugose and tabulate corals, brachiopods, crinoids, ostracods and gastropods.
d) Palaeoenvironment: all localities can be interpreted as protected but strongly open marine conditions of the shallow subtidal zone.

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EVENT CONTROLLED DEVELOPMENT AND DROWNING OF DEVONIAN ELBINGERODE REEF

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Abstract - The Variscan Mid-European Rhenoherzynian zone is rich in Givetian/Frasnian reef complexes. One of the important reefs of the Rhenish trough is the famous atoll-like Elbingerode reef complex. It is situated in the centre of the Harz Mountains. Slate sequences surround and underlie a group of submarine volcanic rises covered by the reefal limestones.

The coral/stromatoporoid reef is distributed over an area of 14 x 5 km containing a wide range of different facies and reef building environments: back-reef, reef core, fore-reef, and off-reef limestones. Investigations of facies distribution in space combined with a detailed conodont stratigraphy have proved a highly complicated scenery of episodic reef growth and changing depocentres of reef limestone accumulation.

The first reef-derived limestones have been accumulated during interruptions of volcanic activities at the basis of Givetian stage (*ensensis*-zone) representing a **pre-phase** of limestone formation. Last volcanic eruptions took place during the lower *varcus*-zone. The real reef development started in the middle *varcus*-zone and continued episodically without any volcanic influence to the end of Frasnian. This reef development (**main phase**) proceeded in three stages (atoll-, cap-, demergence-). Their boundaries are coincident in time with important bio-events: Taghanic event, Frasnian event, Intra-Frasnian event, lower Kellwasser drowning and Kellwasser (Frasnian/Famennian) events.

The lowermost atoll-stage produced the thickest limestones (up to 600 m) in a central lagoon, positioned in the centre of the atoll-like reef structure and surrounded by four volcanoes, each of them fringed by reefs with up to 200 m thick fore-reef debris fans. This stage existed during the whole Givetian between the Taghanic and Frasnian event.

The following cap stage of lower and middle Frasnian is developed in two phases. The depocenters have shifted to the neighbouring synsedimentary active block, because of an endogenic block inversion. The Givetian subsidence of the central block was finished. Reef core and debris sediments of *asymmetricus*-zone accumulated only on the eastern block. During the middle Frasnian *Ancyrognathus triangularis* zone the reef accumulation shifted back to the central block, forming there 200 m of debris and a mud mound.

The rise of sea-level at the beginning of upper Frasnian (lower *gigas*-zone) caused a drowning of reef growth connected with rare deeper water limestones. A new flourishing of reef growth in the upper *gigas*-zone (demergence stage) produced coarse coral-rich debris followed in rare cases by the last

reef-connected limestones (*Alveolitella* floatstones) of the uppermost *gigas* (=*linguiformis*) zone. The facies of these limestones suggests transgressive deeper water conditions indicating a rising sea level. The geological evidence of the Kellwasser-event, the black bituminous "Kellwasser" limestones, are absent on the upper surface of Elbingerode Complex because of the high elevation of the whole reef body. But after this time there are no further coral-bearing limestones. So, the death of reef was immediately connected with the Frasnian/Famennian event.

The facial and stratigraphic facts allow the conclusion, that there were in the Elbingerode reef remarkable correlations between **a)** interruptions of reef growth, **b)** dislocations of depocenters (blocks), **c)** the rate of block subsidence, **d)** and the global bio-events connected with sea level changes. Consequently there should be causal connections between interruptions of reef building, endogenic block movements, events, sea level changes and termination of reef growth.

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NON ANTHOZOAN REEFS

PRESENT-DAY SERPULID REEFS, WITH REFERENCE TO AN ON-GOING RESEARCH PROJECT ON *Ficopomatus enigmaticus*

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Abstract - Serpulids produce a calcareous tube in which they live. Tubes typically encrust any hard substrate but, under certain circumstances, can grow erect attached to each other: they have thus the potentiality of forming huge aggregates. Largest Recent serpulid reefs mainly occur in quiet, enclosed embayments (*e.g.*, *Serpula vermicularis* in Ardbear Lough, Eire) and in brackish habitats (*e.g.*, *Ficopomatus enigmaticus* in the Po River Delta, Italy). Present studies on *F. enigmaticus* reefs in the Magra River estuary (north-eastern Ligurian Sea, Italy) are shortly introduced.

1. INTRODUCTION

The serpulids constitute a large (nearly 300 species) family of sedentary polychaetes: the Serpulidae Johnston. Together with the closely related spirorbids (family Spirorbidae Pillai) they form the superfamily Serpuloidea Bianchi and, together with the Sabellidae Malmgren and other smaller families, the order Sabellida Fauchald (SMITH 1991).

The general morphology of serpulids is similar to that of sabellids, the major differences being the presence of an operculum in the branchial crown of the serpulids (BIANCHI 1981). Such an operculum is either calcareous or chitinous and may be adorned with a variety of hooks or spines. The operculum is used to plug the tube when the worm withdraws (TEN HOVE 1979a).

Like sabellids, serpulids live indeed in a habitation tube, which they cannot leave; however, all serpulids have calcareous tubes, while most sabellids have gelatinous or semihardened organic tubes (only one recently described sabellid genus has a calcareous tube: PERKINS 1991).

Serpulid tubes are usually white, sometimes bluish or pink, and exceptionally transparent. Tube wall structure has recently been described by NISHI (1993). Tubes may frequently bear ornaments, such as pits, keels, tubercles, teeth, ridges, and peristomes (*i.e.*, flaring tube mouths). Unfortunately, not all species have characteristic tubes, and tubes alone may be of little help to identify species.

The tube is secreted by collar glands soon after the serpulid larva has settled on a submerged surface. The tube is almost mineral (calcium plus magnesium) and the collar glands contain a Ca-concentrated secretion (VOVELLE *et al.* 1991, and references therein). The common mineral component of tube materials is calcium carbonate in the form of both aragonite and calcite, in fairly constant ratio for each taxa. Tubes are cemented firmly to any hard substrate (in only few species tubes are free).

Although in the majority of the species the tubes encrust the substrate for all their length, the distal part may eventually detach and grow erectly. Certain species in dense populations build tubes vertical to the substrate in clumps and cement the tubes to each other. This gives serpulids the capability of forming reef-like structures when densely settling. Despite the relative smallness of the individual tubes (rarely longer than 10 cm and wider than 1 cm), such reef-like structures may cover tens of m^2, with a layer more than 1 m thick.

Serpulid reefs are well known in the geological past (FAGERSTROM 1987; SOROKIN 1993), and phenomena of mass occurrence of Recent serpulid species have been reported from many sites (TEN HOVE 1979b; TEN HOVE & VAN DEN HURK 1993).

2. DISTRIBUTION OF PRESENT-DAY SERPULID REEFS

Most serpulids are considered to be 'secondary frame builders', filling crevices and cementing rubble in coral reefs and coralline algae bioconstructions. They act as pioneer organisms, but their role is relatively modest. However, about 30 Recent serpulid species are known to form important aggregates, and may be regarded as 'primary frame builders' or 'welded frame-builders' (TEN HOVE & VAN DEN HURK, 1993). All of these aggregating species occur singly too and thus are not obligatorily constructional. Some species are able to reproduce asexually and thus may form small "pseudo-colonies" (NISHI & NISHIHIRA 1994): these species, however, are not primary frame builders.

According to TEN HOVE (1979b), the major primary frame builders can be divided roughly into three groups, each occupying a major type of habitat and consisting of species that are morphologically (and probably phylogenetically) more similar to one another than to members of the other groups.

The first group consists of taxa that form belts in the intertidal zone of open coasts (*Galeolaria*, *Pomatoleios*, *Pomatoceros* and *Spirobranchus*). The second group is aggregating in quiet, enclosed embayments of normal salinity (*Serpula*, *Hydroides* and *Vermiliopsis*). The third group lives in brackish estuaries and lagoons (*Ficopomatus*).

The largest reefs are formed by members of second and third groups. One example for each of these two last groups will be shortly described in the following paragraphs.

3. THE SERPULID REEFS OF ARDBEAR LOUGH (EIRE)

Ardbear Lough is a glacially formed salt lake located south of Clifden, Connemara, on the West coast of Eire. Here, *Serpula vermicularis* forms large reefs that, having a peripheral distribution, may be described as fringing reefs.

According to BOSENCE (1973; 1979), these reefs covered about 25% of the Ardbear Lough and individually were about 2 m high and several hundred metres across. The reefs were seen to support a diverse and abundant fauna, consisting of encrusters like bryozoans, sponges and bivalves, of predators and scavengers like echinoids and fishes, and of species looking for shelter like decapods.

The factors leading to the aggregation of *Serpula vermicularis* were considered to be a combination of limited substrate, slightly reduced competition for space and possibly high primary production. Larval retention was an important contributory factor leading to the serpulid aggregations.

A serious decline in the *Serpula vermicularis* population was observed over the last number of years, due to dystrophic crises possibly enhanced by increased eutrophication. Such a decline affected population structure significantly, and reefs were almost destroyed (Leahy, pers. comm.).

Two of us (CNB & CM) had the opportunity to dive in the Ardbear Lough, in September 1990 (dives nos 3190 and 4040). As expected, no large reefs were found. However, small buildups of *Serpula vermicularis* were extremely abundant. At 7-8 m depth, erected tubes were growing upwards from large dead fragments of previous reefs laying at the sediment surface. Reef development was apparently following a pattern similar to that already described. However, erected tubes were forming fan-like - rather than bush-like - aggregations. These structures could be interpreted as an early stage of reef formation, due to larval settlement on fallen reef portions. At 12-13 m some spherical or kidney-shaped masses still existed, reaching 50 cm in diameter or more.

4. THE SERPULID REEFS OF SACCA DEL CANARIN (ITALY)

The Sacca del Canarin is one of the brackish lagoons formed by the Po River Delta, in the Northern Adriatic Sea. Reefs built by *Ficopomatus enigmaticus*, a species able to form huge masses in estuaries and lagoons in warm-temperate regions of the globe, were seen to cover about 2% of the bottom of the Sacca with a layer up to 1 m thick, thus reaching the water surface (BIANCHI & MORRI 1994).

It was reckoned that these reefs immobilised more than 30,000 tons of calcium carbonate in the Sacca del Canarin (about 6 km^2 of surface area), and that more than 1,000 tons were produced each year. These figures are consistent with data from north-west Europe estuaries (RULLIER 1946; DIXON 1976).

The framework of the reefs was provided by the rapid growth (up to 30 mm in a month) upwards of crowded tubes. Plasticity of some traits of the worm's life-history, such as the capacity to shift from r to K strategy, and larval retention in confined waters were thought to play a crucial role in reef accretion. Skeletal deposition was extremely high, and periodical collapses due to excessive weight enhanced further settlement and, consequently, compactness of the attachment base. Filling up with sediments, cementation in reducing conditions, and encrustation by the bryozoan *Conopeum seurati* gave adequate rigidity to the tube aggregation: the best developed buildups could withstand the weight of a person. The *Ficopomatus* reefs thus constituted the main hard substrate in the Sacca del Canarin, and provided shelter and resources for nearly all biota, representing diversity islands within the otherwise monotone benthic habitat of this brackish environment.

5. THE ON-GOING STUDIES ON *Ficopomatus* REEFS OF THE MAGRA ESTUARY

Serpulid reefs fall within the scope of the research project CLIMBIOCCA of the Marine Environment Research Centre at La Spezia. CLIMBIOCCA is the acronym of «Influence of CLIMatic change on the activity of BIOConstructional organisms and on their role in the CArbon cycle of the marine environment».

Among the number of marine biogenic constructions occurring in the Mediterranean Sea (LABOREL 1987), three are presently studied within CLIMBIOCCA. These are: 1) the buildups made by the bryozoan *Pentapora foliacea* in the so-called 'coralligenous' formation around the islands of the Gulf of La Spezia; 2) the banks of the symbiotic and colonial hard coral *Cladocora caespitosa* in the eastern Ligurian Sea; 3) the serpulid reefs built by *Ficopomatus enigmaticus* in the Magra river estuary.

The Magra is a small river flowing from the Apennines down to the north-eastern corner of the Ligurian Sea; it terminates with a relatively long, salt-wedge estuary (MORRI *et al.* 1991). *Ficopomatus enigmaticus* is common in most of the estuary, along a stretch of more than 3 km, but is mass-forming only in a small zone of the lower estuary, and especially around the concrete piers of the 'Ponte della Colombiera'.

Ficopomatus reefs occur between 0 and 2 m depth; below, in constantly saline waters, they are replaced by mussel beds. Reefs are extremely dynamic in both space and time, due to the patchy disturbance by the irregular, torrent-like river flow.

Observed densities in reefs range from 70,000 to 180,000 worms / m^2; the average distance between tube mouths is 1.2 mm, and the average tube diameter is 1.6 mm (ALIANI *et al.* 1995). One cubic meter of *Ficopomatus* reef contains about 700 kg of calcium carbonate, 50 kg of which are in the form of fine sediment associated to the interlacing tubes.

Present studies (carried out by SA) are aimed to describe, on the basis of monthly samples and observations, the annual cycle and the structure and formation of the aggregates.

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Y. Leahy (Galway) updated information on the serpulid reefs of Ardbear Lough. J. Vovelle (Paris) critically read the manuscript.

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REEFAL BUILDUPS BY DASYCLADACEAN ALGAE IN THE TITHONIAN OF LANGUEDOC (FRANCE)

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Abstract - During the Tithonian, back-barrier facies are very coarse, with sporadic coral constructions. In these limestones small reef patches occur, constructed only by the dasycladacean algae *Neoteutloporella socialis* (Praturlon) in life position. These constructions are roughly hemispheric, metric to pluri-metric in diameter, half a metre to two metres in height, and have mushroom shape. They have formed on soft gravel substrates. But they allow the settlement of other organisms such as brittle dasycladacean algae. They constitute buildups of pure framestones, surrounded by very coarse calcarenites made of varied fossil debris, including various corals, bivalves including *Diceras*, gastropods with numerous nerineans.

When examined carefully, these constructions are seen to be made of algal thalli always side by side, with a strong tendency towards a fan-like disposal.
Neoteutloporella socialis seems to be the only known dasycladacean algae with a building potential.

1. INTRODUCTION

South of the French hercynian "Massif Central", the Languedoc region was, during the Jurassic, like a hinge between deep environments of the Vocontian Basin eastwards, and shallow sedimentation on a platform westwards (Fig. 1 and 2). This region was characterized by synsedimentary movements of a very shallow ridge, oriented NNE-SSW, periodically emerging, settling a stairstep-like bottom topography descending eastwards.

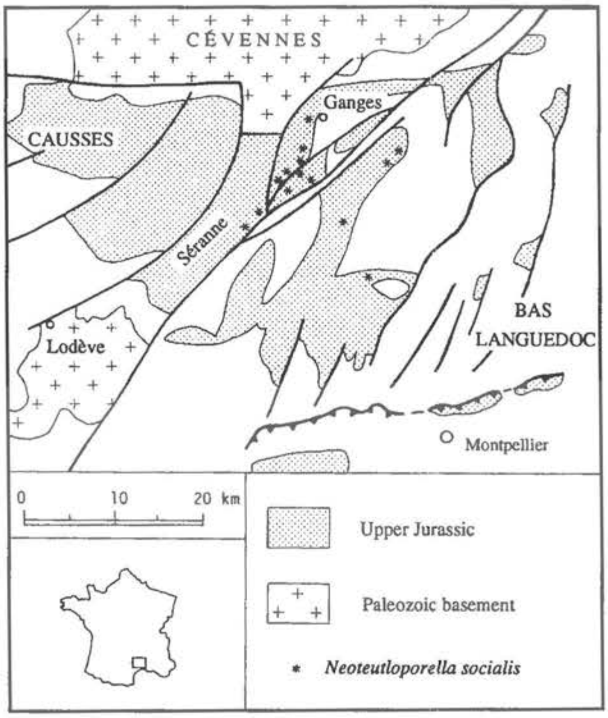

Fig. 1. Location

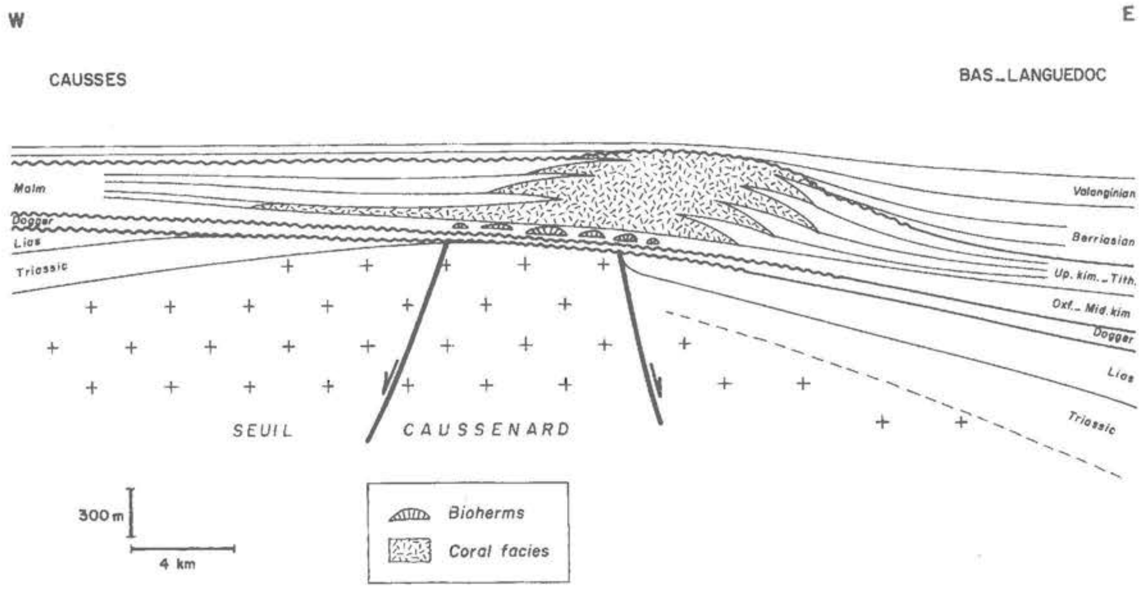

Fig. 2. Synthetic cross-section through the Upper Jurassic ridge in Languedoc.

During the Tithonian, the eastern border of the occidental platform rose as bioaccumulated barrier with scattered coral developments (Fig. 3). This bioclastic barrier played a very important palaeogeographic role: it was fringed, on its eastern margin, by subsiding external slope facies with scattered collapsed corals; its western margin, very shallow and less subsiding, was a zone of considerable development of internal platform facies of loferite type, composed of very coarse stratified limestones, with traces of emergence. Organisms are numerous, but not very varied, and indicate some restriction, although it is not rare to find scattered coral developments or small coral buildups.

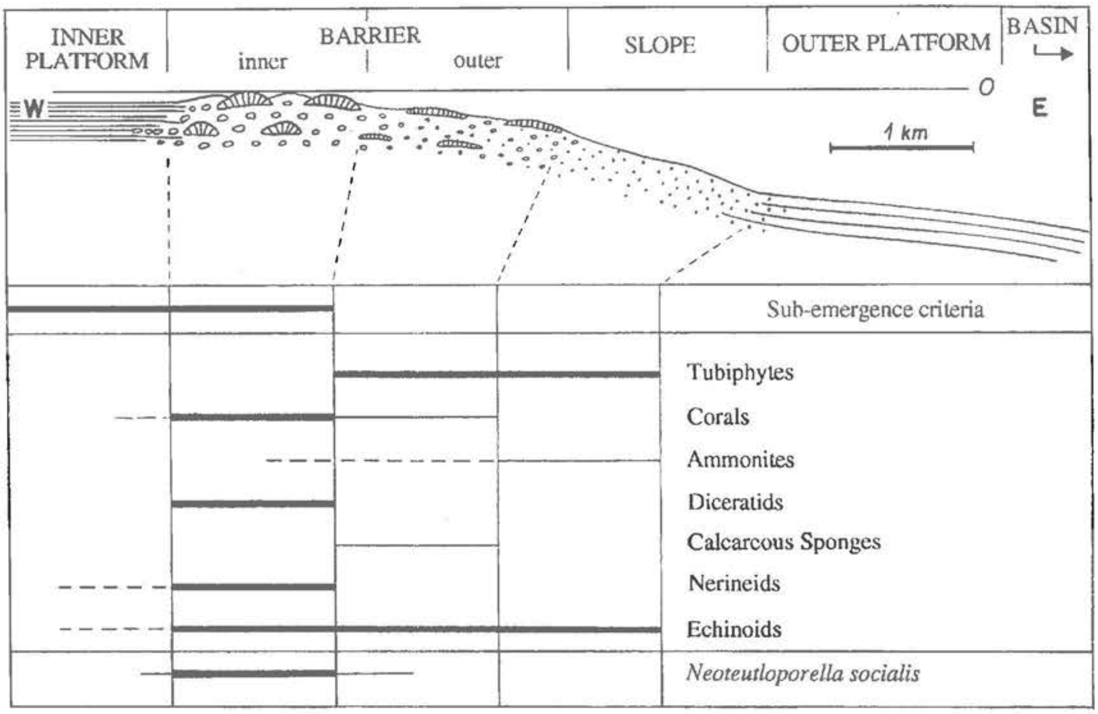

Fig. 3. Cross-section through the Tithonian barrier indicating the location of the alga *Neoteutloporella socialis* with respect to the main facies and groups of organisms.

2. THE BIOACCUMULATED BARRIER

This Tithonian barrier, separating two very different sedimentary domains (Fig. 3), is about 500 metres thick, 2 kilometres wide, and more than 40 kilometres long. It is characterized by considerable *in situ* development of very coarse, massive biocalcarenites, lacking stratification, and with sparitic cement. There are also small sporadic coral masses. On its internal side, this barrier includes diceratid buildups, often associated with finer facies. Organisms are very numerous and varied, little or not reworked : numerous and varied diceratids and bivalves, nerineids and other gastropods, corals, echinoids... They are also very rich in microorganisms among which benthic forams (*Pseudocyclammina, Trocholina*...) and algae such as various dasyclads (*Triploporella, Montenegrella, Petrascula, Clypeina*...) or some encrusting forms (*Thaumatoporella*, Stromatolites). There also occur some incertae sedis organisms like *Bacinella - Lithocodium* which may have contributed to the stabilisation of the substrate. These organisms are sometimes associated with subemergence criteria from the intertidal to the peritidal zones, such as fibrous isopachous cements, keystone vugs, microkarsts... These facies, corresponding to medium to high energy environments, could have been more or less stabilised by building organisms or early cements. It is in these deposits that some building dasyclads can be observed.

3. THE DASYCLADACEAN ALGA *Neoteutloporella socialis* (Praturlon) AND ITS BUILDING ABILITY

This dasyclad, first described by PRATURLON (1963) and later revised by BASSOULLET *et al.*(1978), has been found to date, only in reefal and bioclastic barriers fringing carbonate platforms, in a very localised area : the Alps, Apennines, Dinarids and Carpathian Mountains (DRAGASTAN *et al.* 1987).

The thallus of this very elegant dasyclad is composed of an elongated tube, 2 to 3 millimetres in diameter and several centimetres or decimetres in length (Pl. 1, Fig. 1). This tube is formed by the superposition of very numerous funnel-shaped whorls of branches, making up an angle of 30 to 50 degrees with the axis. Thalli are closely juxtaposed to one another in a roughly parallel pattern, but with a fan-like disposition of their axis. They are welded by their external calcareous crust, at the extremities of some branches. This gives a good resistance to the whole assemblage of thalli, which looks like a colony, having a roughly hemispheric shape. These strongly calcified "colonies" constitute masses of pure framestone. They were probably fairly wave-resistant and acted as shelters for others more fragile algae like *Petrascula, Triploporella, Montenegrella*, that can be found in their vicinity. Small colonies are frequently reworked, while bigger ones are always in growth position, sometimes showing some dissolution cavities (microkarsts ?).

Like other dasyclads, they probably required attachment to solid objects, although traces of their holdfasts are not obvious. They could have been embedded partly in loose deposits, especially when the sediments are more or less stabilised by binding organisms such as *Bacinella* and *Lithocodium.*

In Rumania, DRAGASTAN *et al.* (1987) described scattered bushes of *Neoteutloporella socialis*, 15 to 17 centimetres in diameter, that these authors qualified as "reefal". Previously BODEUR (1980) had briefly indicated some bigger examples of the same algae.
According to their complexity, one can distinguish two types of "colonies" :

1) Individual bushes, 10 to 50 centimetres in diameter :

When they are not constrained in their growth by competition by other organisms or with a rapid sedimentation rate, these algae exhibit a flat mushroom-like form, increasing the basal surface of the "colony", in order to prevent it from being overturned by waves or currents (Fig. 4, B-C).

When these bushes occurred in an environment with a high rate of sedimentation, they have a tendency to grow rather vertically and the "colonies" then, show a massive hemispherical shape (Fig. 4, A).

2) Superposed groups of bushes, growing on each other in an irregular pattern, can occur. The resulting bulk, more than one metre in diameter appears as an irregular knoll (Fig. 4-D and Pl. 1, Fig. 2). This type of construction must have been very well anchored in their gravel substrate. They are linked with medium to low sedimentary rates, and medium energy conditions.

They occur immediately behind the barrier, in quiet microenvironnents, on more or less stabilised substrates.

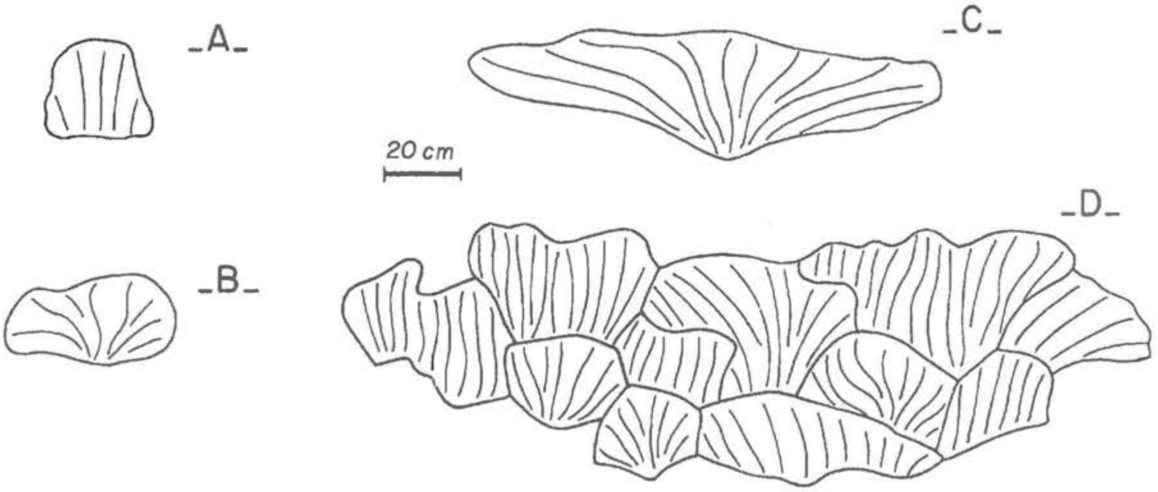

Fig. 4. - A - Flat hemispherical form of some bushes of *N. socialis.*
- B - Fan-like disposal of some thalli of *N. socialis.*
- C - Flat mushroom form of some bushes of *N. socialis.*
- D - Superposed bushes of *N. socialis* resembling irregular knolls.

4. CONCLUSION

In the Tithonian of Languedoc (France) the relative abundance of the dasycladacean algae *Neoteutloporella socialis*, and its building ability, suggest that they found here very favourable ecological conditions in some particular microenvironments within these extensive, very shallow, and high energy bioclastic deposits.
These algae seem to be, until now, the only known dasycladacean algae with a building potential.

ACKNOWLEDGEMENTS - to P. Bernier, F. Brochard, N. Chevillotte, A. Cossard, F. Epaulais, P. Génot, M. Hauray, B. Purser, for their technical or scientific help, especially in improving the manuscript.

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Plate 1

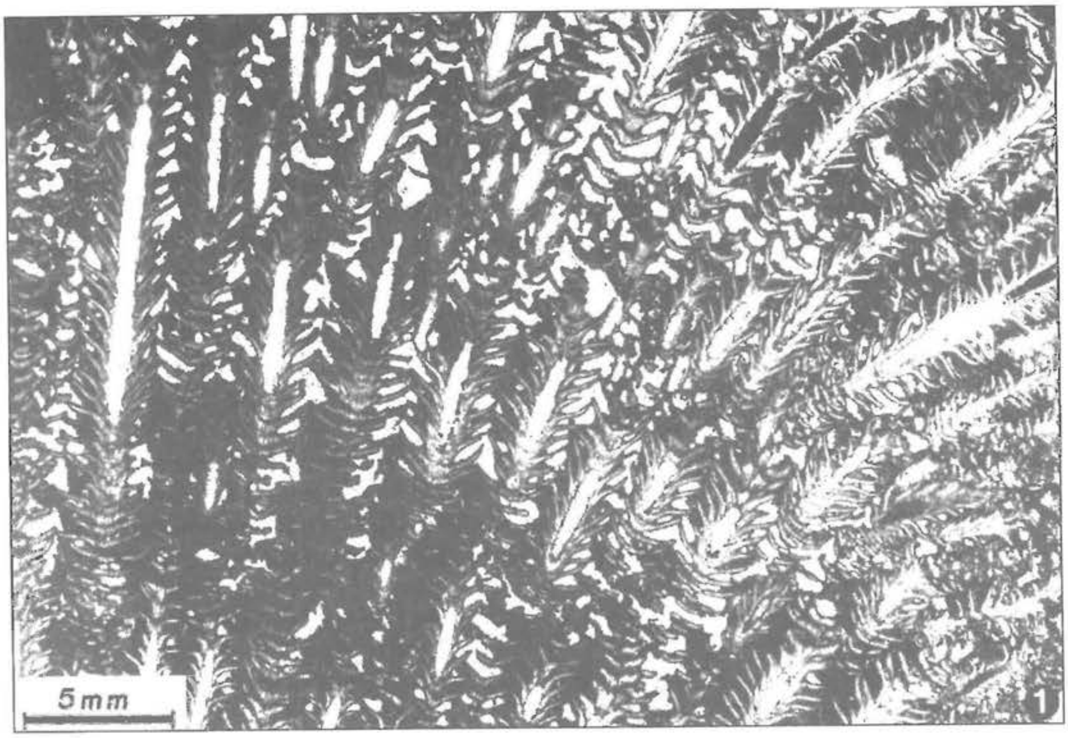

Fig. 1. Thin section in a framestone of *Neoteutloporella socialis* (Praturlon). Tithonian of Languedoc (France).

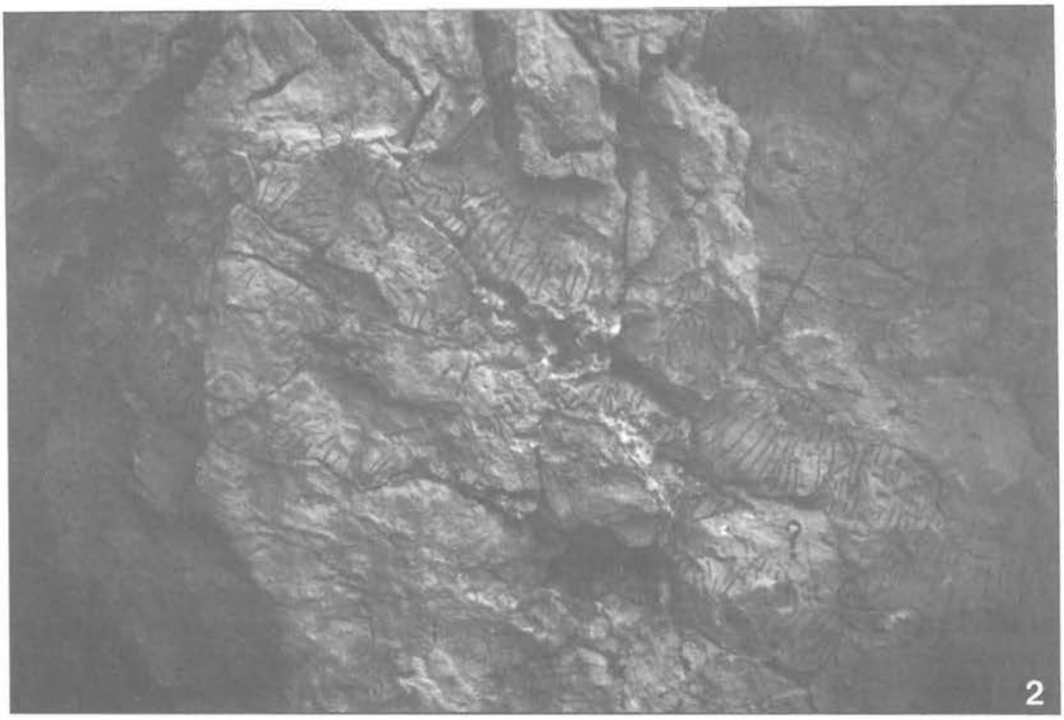

Fig. 2 . Superposed bushes of *N. socialis* forming an irregular and overturned knoll. The main growth directions of the thalli and the outlines of the colonies are underlined with a marker, directly on the outcrop, in order to make them visible.

ECOLOGICAL CONDITIONS OF MODERN SABELLARIAN REEFS DEVELOPMENT: GEOLOGICAL IMPLICATIONS

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Abstract - Important reefs are built on European coasts by the polychaete *Sabellaria alveolata* (LINNÉ). Modern and fossil Sabellariids are characterized by their tube structure. The different types of colonisation, reef morphologies and growth phases give information about physical factors such as the hydrodynamic regime. A major direction of development is suggested by the lengthening of the constructions.

1. INTRODUCTION.

At present and on a world-wide scale, sabellariids have a distribution reaching from the surface to hundreds of meters water depth. Gregarious species growing in reefs, however, are littoral living from 0 to about 20m deep, most often intertidal ; they occur in temperate to tropical waters. We looked at examples of reef growth on the European coasts, where *Sabellaria alveolata* lives in the intertidal zone (Fig.1) or some meters deep. Can the morphology and the orientation of the reefs give useful information on ecological factors?

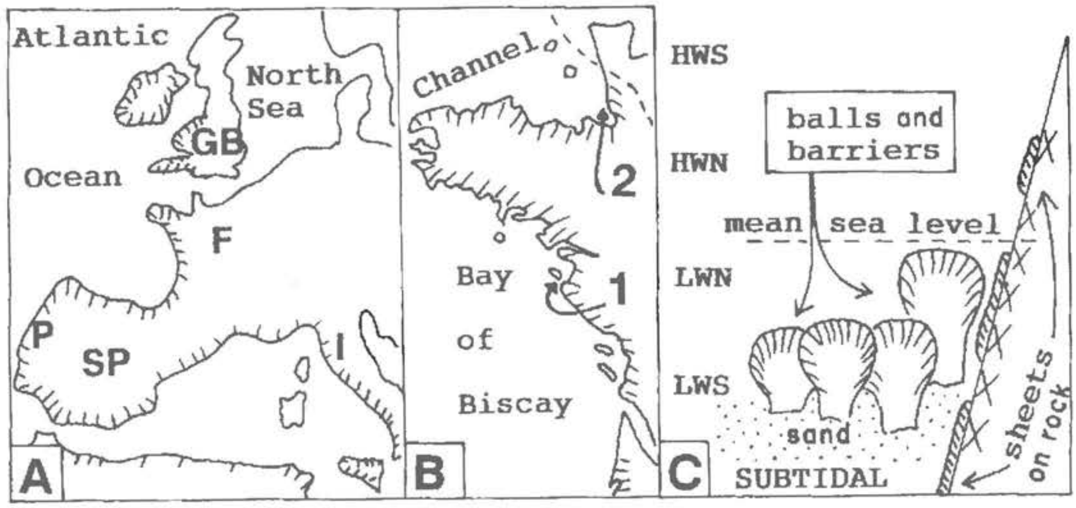

Fig.1. A: geographical distribution of *S.alveolata* in Europe (shaded coast) . B: location of studied reefs , Bay of Bourgneuf (1) and Bay of Mont-Saint-Michel (2). C: vertical distribution of reefs. HWS and LWS: high and low water spring tide. HWN and LWN: high and low water neap tide.

2. SETTLEMENT OF YOUNG WORMS AND GROWTH OF THE TUBES.

In the zoogeographical region of *S.alveolata*, which extends from the western Channel to Mauritania, males and females breed to produce long-living larvae. These must find hard substrates to settle: this is the primary settlement phase (Fig.4 and GRUET 1986). Nature and size of the substrate may vary, but it must be stabilised enough to keep the worms alive. On exposed shores such as in North Devon (WILSON 1971), it can only be rock. On sheltered shores, the substrate can be a small pebble (Plate I, photo 7; Bay of Bourgneuf, GRUET 1971-72) or a shell (Bay of Mont-Saint-Michel, CALINE *et al.* 1988). Larvae also settle on and between the tubes of adult worms: this is the secondary settlement (Fig.4 and Plate I, photo 4) ; (GRUET 1986). PAWLICK (1988) discusses a possible attraction by chemotactism which could be the main explanation for the gregariousness of the species.

Settlement occurs also on broken and moved reef blocks. It is a factor of horizontal extension and explains how an extensive reef such as the "Banc des Hermelles" (Mont-Saint-Michel bay) could develop without any visible rock substrate.

3. GROWTH AND STRUCTURE OF THE TUBE.

S. alveolata builds with sand chosen just around the aperture of its living tube. There is a good calibration of grains according to their shape (GRUET & BODEUR 1994) and their size (300 to 800 microns). Diameters of the grains are linked by a statistical relation to the height of the building organ (GRUET 1984) and also depend on the age of the worm. Grains are glued together by meniscus cement rich in P, Ca and Mg (GRUET *et al.* 1987). Bioclasts are arranged in three layers: a first one of regular pavement, a second thicker layer arranged in funnel shape, and a third including the infillings between the funnels (Fig.2A-B).

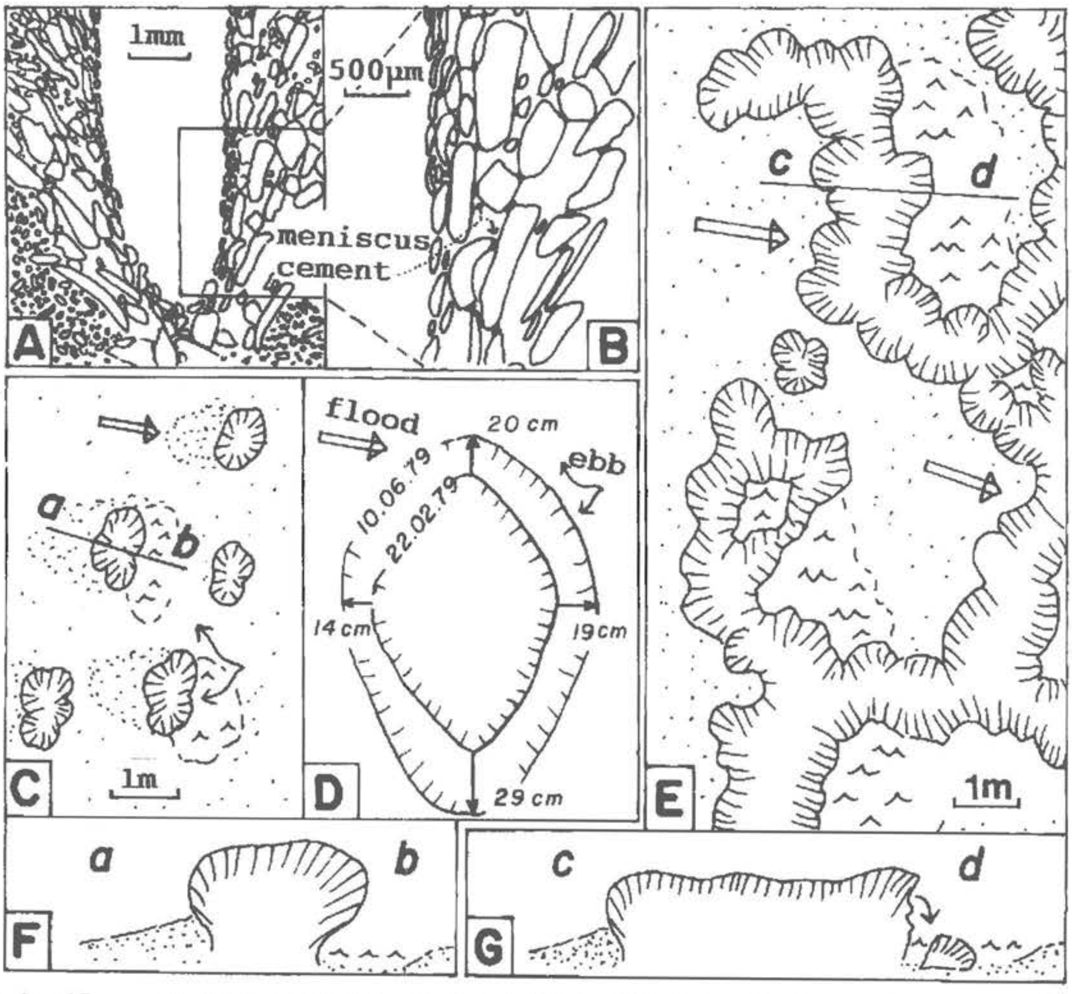

Fig.2. A and B: structure of the tube (see also plate I, photo 8). C to E: isolated constructions and horizontal growth in less than 4 months (4). F: reef with barrier and platform stages, section view (G).

4. MAIN PHASES IN THE DEVELOPMENT OF SABELLARIAN REEF MORPHOLOGY.

We have considered only colonies forming reef structures independently of rocky substrate. In sandy environments, the reefs have a better chance to become preserved as fossils. Why does *S. alveolata* build tubes as long as 20 to 40 times its own body length? The growing animal needs a constantly widening tube. Also, the worm must be able to move inside its tube (15 to 20cm) in order to get oxygenated and push out its faeces. In experiments the animal builds its tube faster at high temperature. Under natural conditions, however, rates of construction (GRUET 1971 -72) are higher in winter, autumn or spring when currents are strong during storms or spring tides. Sand moving just beside the worm seems to be the main factor stimulating the building activity. Construction and erosion of the tubes can give a morphological development with different stages succeeding in one cycle of several years (GRUET 1986).

4.1. Growth phase with formation of balls (decimetric scale) (Fig.2 and plate I, photo 2).

The tubes grow first horizontally, then vertically, resulting in ball-shaped constructions. Secondary settlement helps to increase vertical growth in a more or less symmetrical fan shape when viewed in section. In zones where dominant waves have the same direction as the flood tide, the construction lengthens in a direction perpendicular to the main current. On the exposed side, growth can be reduced to give an asymmetrical form. Under extreme hydrodynamic conditions, tubes can grow obliquely, adjusting their apertures to face the sheltered side.

4.2. Growth phase with formation of barriers (metric scale) (Fig.2).

Balls join together due to secondary settlement (Plate I, photo 4). Growth rates of the tubes can be very fast in balls close to sand surface (20cm in a month) and low at the top of the same balls (1 to 4cm). Barriers can have an asymmetrical form in section. Sand can accumulate during flood tide on the exposed side of the reef ; on the opposite side, we commonly find a pool. The general direction of growth is perpendicular to the main currents and swells. Some of these barriers can develop across channels, modifying their flow.

4.3. Growth phase with formation of platforms (decametric scale) (Plate I, photo 1).

Barriers can join to create a platform. Growth is slow. The top of these constructions is flat, often covered with algae. The reef has a reticulate form with sand accumulations on exposed sides and pools on opposite sides. This morphology is well developed when the hydrodynamic regime is strong. We see then one “active” direction with others more or less perpendicular. In some cases destruction and growth with new settlements simulate a horizontal migration (Fig.3, E to H). In other cases, the reef may disappear under the sand and develop again in a superposed construction (Fig.3, A to D and plate I, photo 3).

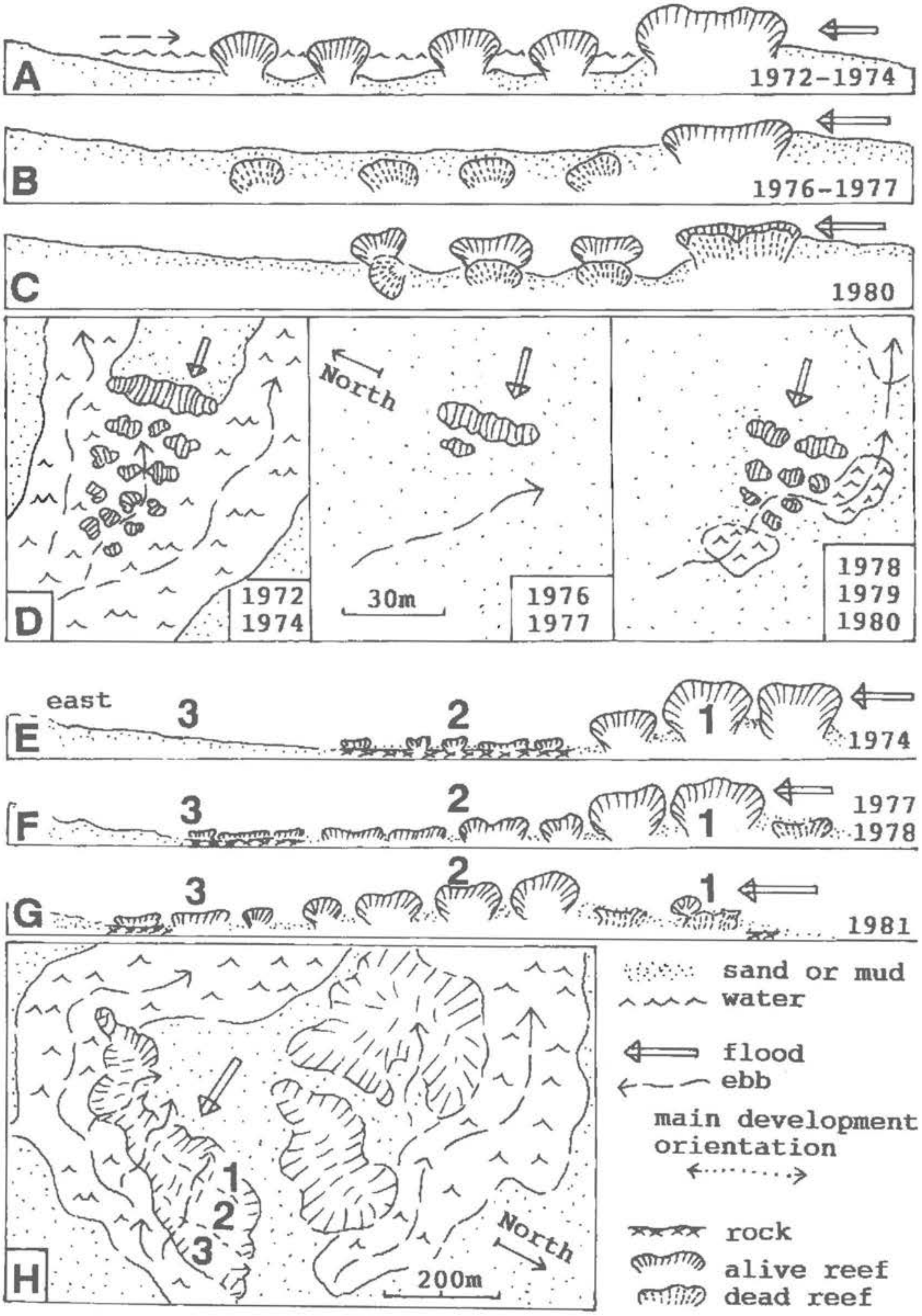

Fig.3. *S. alveolata* reefs in the tidal delta of Fromentine (Island of Noirmoutier, France). A, B, C and D: development of superposed reefs; E, F, G and H: reefs migrating horizontally (see also plate I, photo 5 and 6).

4.4. Reefs or banks (hectometric scale).

Outer limits and general orientations of reefs have different meanings. They can simply correspond to the rocky substrate, or the reef moves according to the hydrodynamic regime and independently of the substrate. Sand dunes then move across the reef. Sediment is stabilised by the growing reef and mobilised when the reef is destroyed. The reef behaves like a filter, becoming partially blocked by sand. The reefs of the Fromentine delta (Noirmoutier, France) are composite but generally substrate-oriented. On the contrary, the orientation of the "Banc des Hermelles" (Mont Saint-Michel bay, France) is only controlled by hydrodynamics and sand dunes.

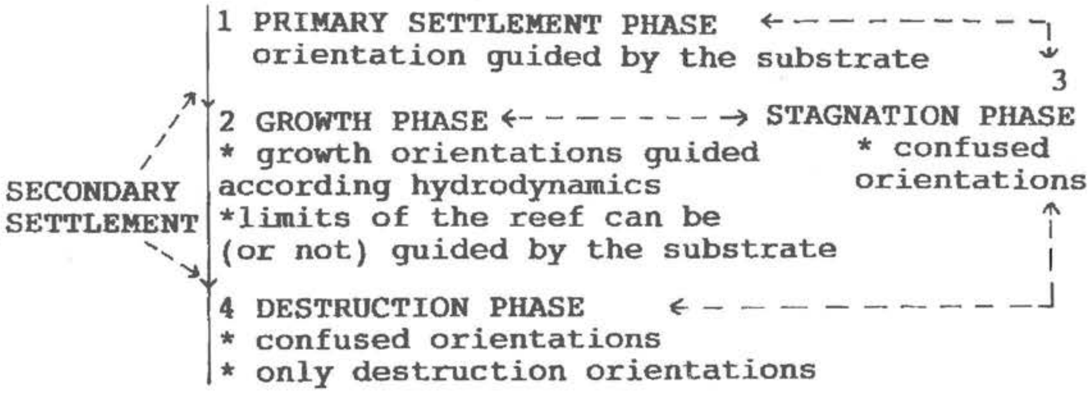

Fig.4. Main phases of sabellarian reef development and orientations of the constructions (see also GRUET 1986).

5. CONCLUSIONS.

Sabellarian reef morphology is the result of a constantly disturbed and precarious balance between biological and physical factors. Succession of the different phases mainly depends on two factors: hydrodynamics and larval recruitment. However, physical factors associated with the current and wave regime generally dominate and control the evolution. REISE (1991) includes the successional cycle of Sabellarian reefs in the more general mosaic-cycle concept of ecosystems. These reefs can be preserved as fossils especially in sandy environments such as tidal or estuarine deltas. Until now, as far as we know, only one fossil occurrence (GARCIN & VACHARD 1987) has been recognized as a Sabellarian reef. Therefore, examination of modern reefs of *S. alveolata* gives the opportunity to determine some geological consequences. The study of the substrate of fossil reefs gives information on the hydrodynamic factors, small substrates as pebbles or shells being found only on sheltered shores. The structure of the tube with a funnel shape is characteristic of the sabellariids and has been found in fossil examples. Symmetry and lengthening of constructions give an idea of the main direction of currents and sand movement. Hydrodynamics, sand and substrate thus play an important role in reef development.

ACKNOWLEDGMENTS. Gratitude is expressed to Dr J. Geister and to B. Bernard for improving the English text, to Dr A. Strasser and Dr H. Hüssner for their useful remarks on the manuscript. We thank Alain Cossard (University of Nantes) for the developing of the photographs.

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Plate 1

Photo 1. General view of a part of the sabellarian reefs in the tidal delta of Fromentine (Noirmoutier island, Vendée, France). In front, stages of balls growing more or less quickly. At top stages of platforms with a stagnating growth (see text in 4.2 and 4.3).

Photo 2. Stages of balls growing fast and giving stages of barriers. Scale provided by the isolated construction in the center, 1.20 meter width (see text in 4.1).

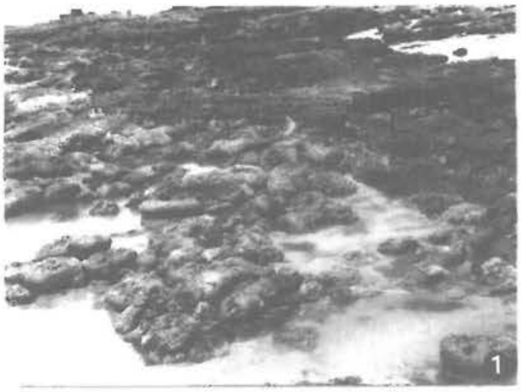
Photo 3. Superposed reefs. Worms of the inferior balls have been killed by sand covering them during several months (see text in 4.3). Scale provided by the notebook 17cm long.

Photo 4. Close view of a construction showing large tubes (worms ageing several years) and small tubes (worms ageing one year or less). This massive "secondary" settlement has filled crevices and has contributed to the growth of the construction (see text in 2).

Photo 5 and 6. Same reef area after a period of one year and eight months (5 in april 1979, 6 in january 1981). See figure 2 , F and G. Scale provided by iron table 2 meters long.

Photo 7. Small constructions settled on pebbles on a sheltered beach (see text in 2).

Photo 8. Longitudinal view of a broken tube showing the funnel shape pattern of bio-clasts. The opening of the tube is at the top (see figure 2, in 1 and 2).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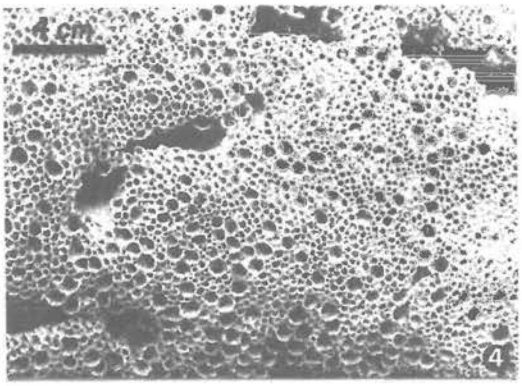
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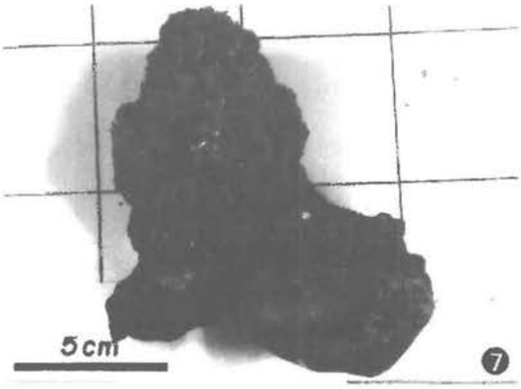
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THE ROLE OF SKELETAL AND NON-SKELETAL COMPONENTS IN THE SARMATIAN (MIOCENE) REEFS OF POLAND

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Abstract - Peloidal limestones of microbial origin and early submarine fibrous cement are, by volume, the most important constituents of the Sarmatian reef rocks in Poland. Serpulid tubes occur throughout the reef but are only of secondary importance. Encrusting cheilostomatous bryozoans, sessile forams *Nubecularia*, and monostromatic red algae, which sometimes form separate mini-bioherms, usually form only thin crusts on the main microbial limestone bodies. Such an unusual reef composition is related to the highly alkaline and calcium-rich waters of the enclosed Sarmatian basin.

1. PALAEOGEOGRAPHIC AND STRATIGRAPHIC SETTING.

The Sarmatian (Upper Miocene) reefs which are found in the whole Central Paratethys region (PISERA in press), occur in Poland along the northern shores of a sea that occupied the Carpathian Foredeep (Fig. 1 and AREŃ 1959; BRZEZIŃSKA 1961; KRACH 1962; BIELECKA 1967).

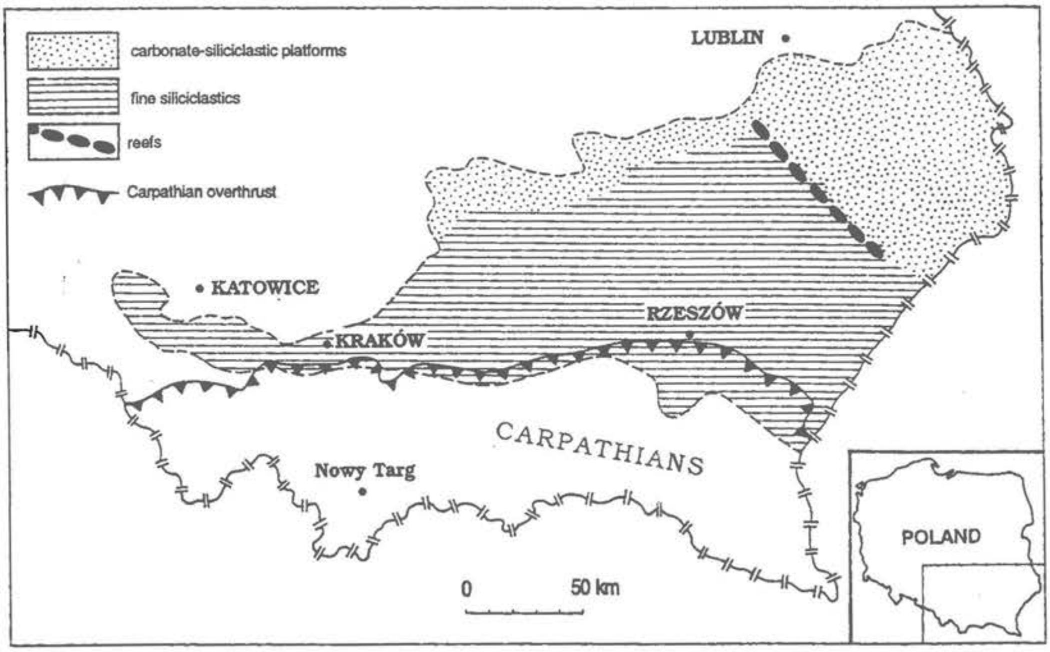

Fig. 1. Palaeogeographic position of the Sarmatian reefs in the Carpathian Foredeep Sea (after NEY *et al.* 1974, modified). Reef widths not to scale. The area shown on the map is rectangled in the inset.

The reefs were established on a discontinuity surface marked by conglomerates of the local Middle and Upper Miocene rock in proximal areas (Fig. 2), and at most distal sites there is a continuity of sedimentation between underlying Middle Miocene bioclastic limestones and the reef. In this latter case, there is a sharp facies change over several centimetres from grainstones to marls, above which the reef started to grow. This depositional sequence suggests that the reefs are part of an overall transgressive system. No deposits overlying the reefs are preserved (Fig. 2).

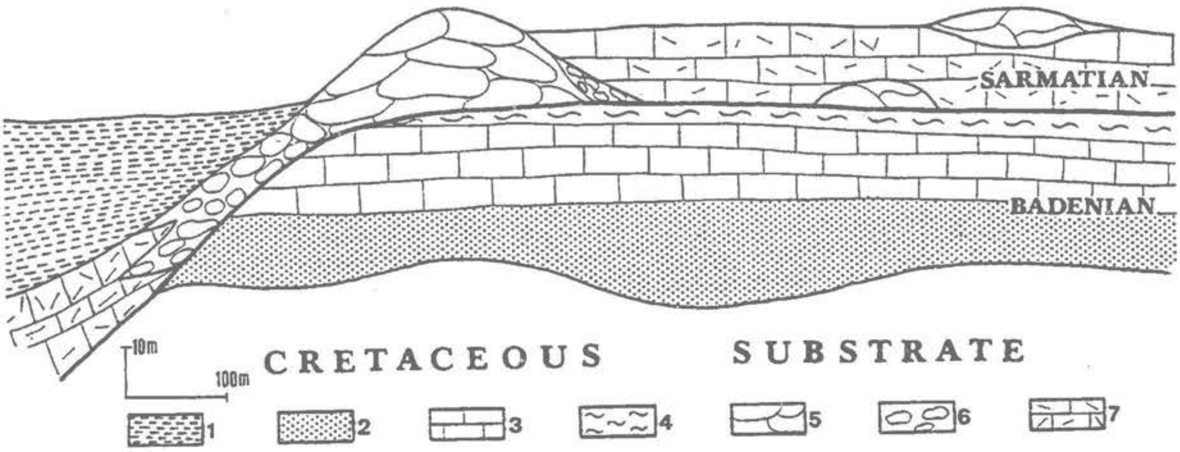

Fig. 2. Idealised cross-section showing stratigraphic position and sedimentary relationships of the reef bodies (from PISERA 1995, in press).
1. Sarmatian siliciclastics 2. Badenian sands 3. Badenian red-algal limestones 4. Badenian marls 5. Sarmatian reefs 6. Conglomerates composed of reef-rock pebbles and blocks 7. Sarmatian detrital limestones.

Large (up to 15 meters thick and several hundred meters long) reef complexes follow the former edge of a very shallow-water carbonate, or carbonate/siliciclastic platform (BIELECKA 1967; LISZKOWSKI & MUCHOWSKI 1969; PISERA 1978) where different types of red-algal (mostly detritic) sedimentation prevailed. Thick sequences of fine siliciclastic sediments infill the basinal part of the Carpathian Foredeep (Fig. 1, 2). Smaller individual reef bodies, up to 2 metres thick, occur dispersed among bioclastic limestones on the platform behind large reef complexes (Fig. 2). Internally the reef complexes are composed of smaller stacked, up to 2-3 metres large, individual reef bodies separated by thin marly intercalations, most probably of storm origin (Pl. 1: 1). In the fore-reef, slightly deeper than the reef-complexes themselves, conglomerates of reef-rock (with blocks reaching 50 cm in diameter) have accumulated.

2. PETROGRAPHY OF THE REEF ROCK.

The reef rock is not bedded and very porous (Pl. 1: 2) with internal sediments infilling numerous growth cavities (Pl. 1: 3, 10). It forms lenticular to irregular bodies, often with clear internal zonation. The outer portion of the individual bioherm, usually several centimetres thick is composed of sessile forams *Nubecularia* (Pl. 1: 6) and/or monostromatic red algae *Lithoporella* and *Titanoderma* (Pl. 1: 7) with admixture of serpulid tubes (Pl.1: 6), and sometime also encrusting bryozoans *Schizoporella*. Serpulid tubes are sparsely distributed throughout the entire bioherm (Pl. 1: 2, 5, 6, 10), while in the fore-reef they may form a serpulid biolithite, in which serpulid tubes are cemented only with a thin fringe of early fibrous cement (Pl. 1: 4). *Schizoporella* forms also a few small (up to 2 metres in size) separate bioherms. The main body of the bioherm is composed of microbial limestone (Pl. 1: 3) consisting of thrombolitic (Pl. 1: 10) and stromatolitic (Pl. 1: 9) structures composed of peloids (cemented with fibrous to bladed early submarine cement), with varying proportions of the thick early submarine fibrous cement (Pl. 1: 8, 9). The peloids are round to rod-shaped and measure from 20 to 60 µm; often they form compound bodies which contain several peloids of this size enclosed within a thin micritic envelope. Centres of the bioherms may contain more cement than peloids (Pl. 1: 5, 8).

3. DISCUSSION.

The composition of the reef rock and the associated molluscan fauna as well as the absence of any stenohaline organisms indicate that water chemistry strongly deviated from normal marine conditions during the reef growth (PISERA 1990). The peloids which occur as internal sediments and within the thick encrustations of fibrous cement are identical and may be considered as peloidal cement known from Recent reefs (MACINTYRE 1977; 1984; 1985; MACINTYRE & MARSHALL 1988; MACINTYRE *et al.* 1990). Those peloids which compose most of the biohermal body, are more closely resembling (especially their aggregates) calcified coccoidal cyanobacteria. Taking into consideration this and the thrombolitic and stromatolitic structure of the reef limestones, I interpret these limestones as a microbial product. Most probably they originated in a highly alkaline environment (and rich in calcium as indicated by importance of early submarine cement), as such conditions usually support thriving calcifying cyanobacterial communities, which were responsible for microbial limestone formation. No close Recent analogues of these Sarmatian reefs are known; they may be compared, however, to the bryozoan and stromatolite reefs from brackish lakes from Netherlands (BIJMA & BOEKSCHOTEN 1985) and/or stromatolite and red-algal reefs from the alkaline lake in the Santonda Crater, Indonesia (KEMPE & KAZMIERCZAK 1993). Among fossil examples the Permian bryozoan reefs from England (SMITH 1981) are very close, both in structure and composition.

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Plate 1

Fig. 1. Small, about 2 x 1.5 m large, individual bioherm from the main platform-edge reef complex. Potoczek.

Fig. 2. Details of the reef-rock showing its high porosity and numerous internal sediments. Scale bar 5 cm.

Fig. 3. Thrombolitic-stromatolitic "biolithite". Note numerous internal sediments (white and light grey) filling growth cavities. Scale bar 2 cm.

Fig. 4. Part of the reef rock from the reef front composed predominantly of serpulid tubes cemented with early fibrous submarine cement. Łysakow. Polished slab. Scale bar 1 cm.

Fig. 5. Reef-rock composed of very sparse serpulid tubes surrounded by thick encrustations of early submarine fibrous cement (dark); primary pores and rare internal sediment white. Łysakow. Polished slab. Scale bar 2 cm.

Fig.6. *Nubecularia* biolithite with sparse serpulid tubes and cheilostomatous bryozoans. Łysakow. Thin section. Scale bar 5 mm.

Fig. 7. Monostromatic red algae *Titanoderma* from the outer envelope of the bioherm. Gora Chelmik. Thin section. Scale bar 0.5 mm.

Fig. 8. Cement-serpulid "biolithite" (the same specimen as in fig. 5). Łysakow. Thin section. Scale bar 5 mm.

Fig. 9. Stromatolitic fabric. Łysakow. Thin section. Scale bar 5 mm.

Fig. 10. Thrombolitic "biolithite" with peloidal internal sediment and serpulid tubes. Łysakow. Thin section. Scale bar 5 mm.


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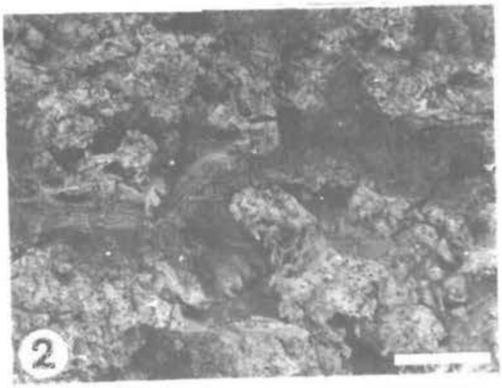
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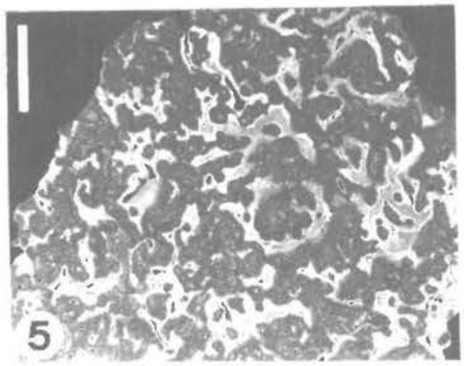
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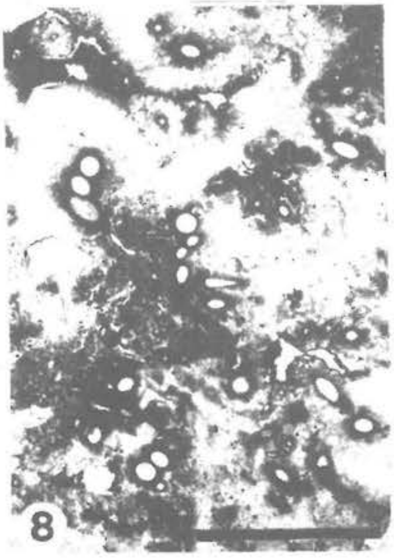
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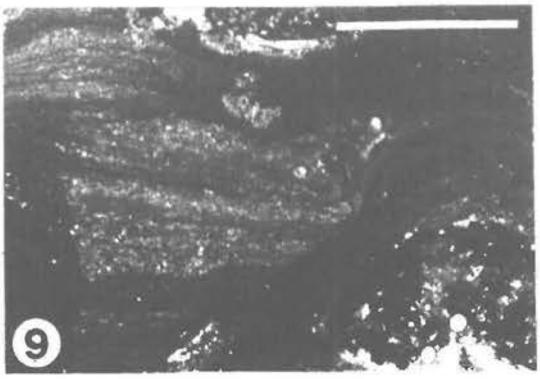
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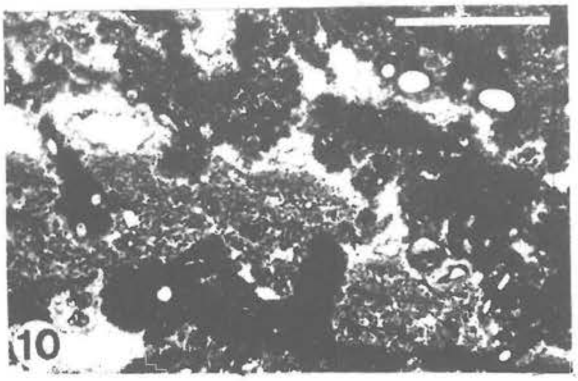
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ON THE DECREASE OF SABELLARIAN REEFS ALONG THE GERMAN NORTH SEA COAST

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Abstract - Extensive reefs of the polychaete *Sabellaria spinulosa* used to occur frequently in the subtidal and occasionally in the tidal zone of the German Wadden Sea. Reports from the literature and from local fishermen date back to the end of the last century. The decrease of sabellarian reefs started 50 years ago. Today only three have remained. The activities of the local shrimp fishery were suspected to have caused the decline by destroying the reefs with their bottom trawls mechanically. In order to elucidate this hypothesis field investigations in the subtidal of the German Wadden Sea were carried out by means of underwater video. In addition, experimental fishing was carried out on a reef of *Sabellaria alveolata* at the French Atlantic coast. No indications were found that the beam trawls of the shrimpers can cause sufficient damage to destroy reef buildings. Controlling factors of sabellarian reefs are discussed. Changes in the hydrological regime due to coastal engineering (dike buildings, dredging) are the most likely reason for the drastical decrease in the German Wadden Sea.

1. SABELLARIAN REEFS IN THE WADDEN SEA

Sabellarian reefs are biogenic constructions of the tube-building polychaete *Sabellaria spinulosa* Leuckart, 1849. The tube consists of sand grains. A single reef can extend to several hectares and is made of thousands of cubic meter of sand. Along the coastline of the German North Sea sabellarian reefs used to occur frequently in the Wadden Sea proper. The Wadden Sea is characterized by extensive tidal flats. During low tide about two thirds of the sea bottom are exposed. Mean tidal range is 1.5 to 4 m. Tidal currents can reach 1 to 2 m/s, but during storms much higher values can be observed. Only small tidal creeks and deeper tidal channels contain permanently water. Reefs of *Sabellaria spinulosa* can normally be expected to occur along the slopes of the deep tidal channels (REISE *et al.* 1989) at water depths of 10 to 20 m and in strong water current. To date reefs have neither been reported from the Danish nor from the Dutch Wadden Sea, but only from the German part.

According to local fishermen 50 years ago reefs were numerous and extensive. Many reefs in the subtidal are reported in the literature from the first half of this century (Fig. 1: black circles). Recently, most of these places were revisited and the sea floor was searched during surveys with dredges, echo sounders and underwater video. The intertidal reefs (Fig. 1: light circles) that have been reported by RICHTER (1927) and LINKE (1951), disappeared completely. Only three reefs in the subtidal remained (Fig. 1: black squares).

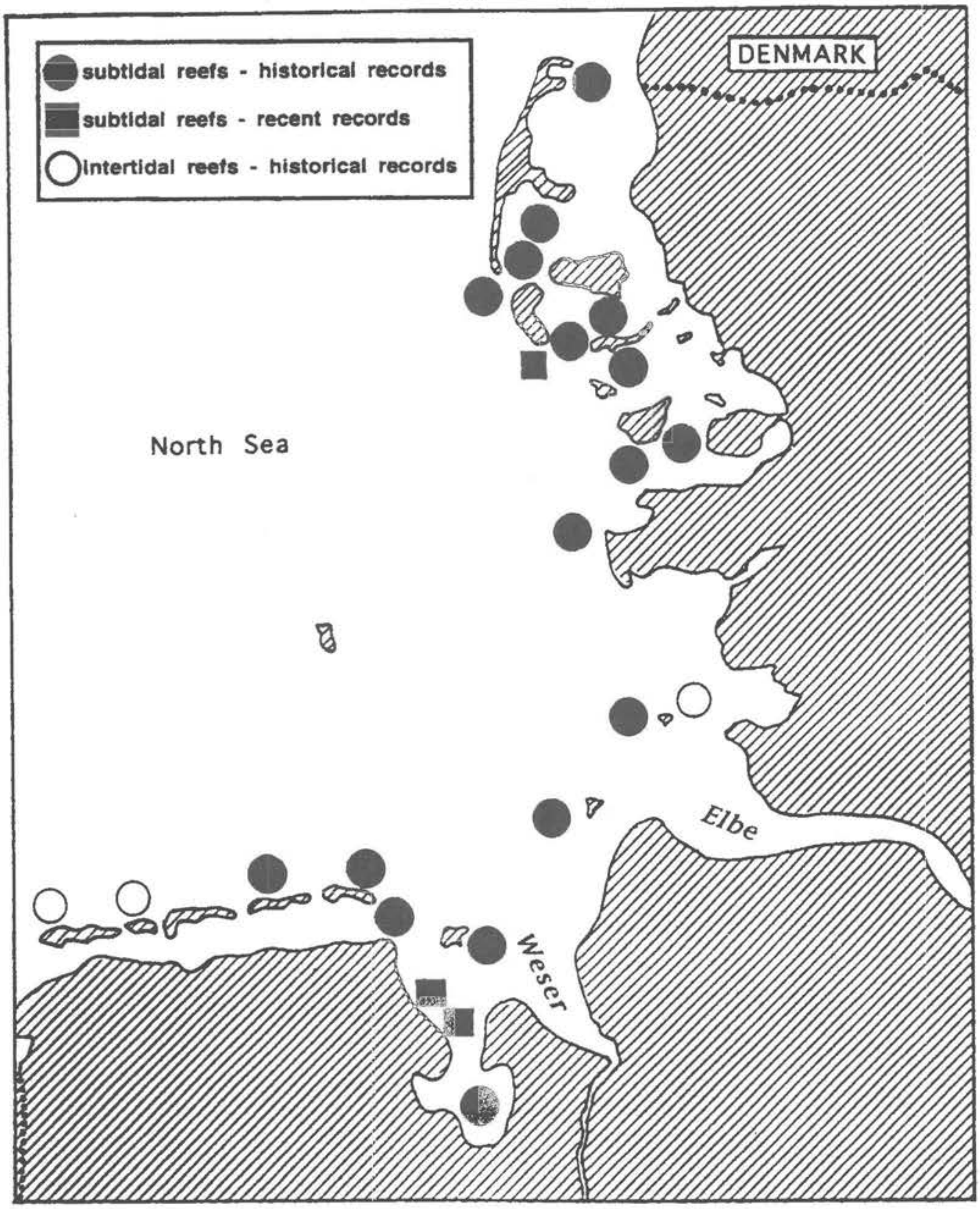

Fig. 1. Occurrence of sabellarian reefs along the German North Sea coast in former times and today.

2. CONTROLLING FACTORS

The natural succession in reefs of *Sabellaria alveolata* in Great Britain (WILSON 1971, 1974) and France (GRUET 1972; 1986; CALINE et al. 1992) is characterized by phases of (1) rapid growth after the origin and (2) by stagnation followed by (3) destruction. This succession has to be kept in mind if the impact of natural vs. man-made factors on sabellarian reefs shall be evaluated.

2.1. Biotic factors

2.1.1. Larval supply

The development of a reef starts with the settlement of larvae on adequate substrate, *e.g.* rocks, gravel, hard sand, or mussel-shells. Its establishment depends on continued larval settlement since it takes several generations to build up a reef. Consequently, low densities of larvae will fail to initiate a reef or introduce stagnation. Plankton investigations in the German Bight at the island of Helgoland revealed regular occurrence of larvae of *Sabellaria spinulosa* every year in August and September (HUSEMANN 1992). The amount of larvae varies considerably from one year to another year (10 individuals per m^3 in 1989 to more than 100 in 1990).

2.1.2. Enemies

Sabellarian reefs are very stable. The worms can quickly draw back into their tubes and are well-protected against enemies. Only few predators are able to capture a worm. In aquaria crabs like *Carcinus maenas* and *Cancer pagurus* crush the tubes and feed partly upon the worms. Under natural conditions they go for other food and predation effects are of minor importance to the reef.

2.1.3. Competition

Competition for food and space with other sessile benthic species is not relevant as long as the sabellarian reef is in good condition. A well-growing reef is rarely covered with barnacles, mussels or algae. However, a reef in (natural) stagnation and/or destruction may offer substrate e. g. for blue mussels (*Mytilus edulis* , LINKE 1951) which will enhance its destruction.

2.2. Abiotic factors

2.2.1. Settling ground

An important prerequisite for larval settlement and the origin of a reef is hard substrate. Apart from rocks, stones or mussel shells any already existing sabellarian reef (dead or living) is the preferred settling ground. The larvae are able to detect biochemically old worm tubes which have been built by the same species (PAWLIK 1992).

2.2.2. Water current

Growth of a single worm and of the whole reef is highly dependent on water currents providing both food and sediment particles for tube-construction. Changes in current speed and direction may have different effects. Higher current speed increases erosion, whereas low current speed increases sedimentation. In both cases sabellarian reefs may be negatively affected. High erosive forces destroy the reef while high sedimentation rates may bury worm tubes. However, even a stable current regime cannot guarantee an everlasting reef. A well-growing reef will sooner or later reach a critical height, where the water currents are not strong enough to supply the upper part with sediment particles (CALINE *et al.* 1992). Consequently, further growth is not possible and the reef enters the stagnation phase. Subsequently, parts of the reef will slowly die. During this phase the reef is susceptible to the erosive forces of water currents and destruction is only a question of time.

2.2.3. Climate

Temperature and weather conditions can affect all phases of development in different ways. Water temperature influences the activity of the worms. Thus, the warmer season is the main growth period. Reduced wind and thereby reduced wave action during calm summer periods can stop reef growth, while stormy weather in mild winters can promote reef growth. In contrast, cold winters can cause high mortality of worms and heavy weather can destroy the reef. Concerning these climatic factors, optimal conditions for a sabellarian reef are found in autumn, when temperatures are moderate and turbulent wind provides turbid water.

2.3. Anthropogenic effects

2.3.1. Fishery

RIESEN & REISE (1982) were the first to put forward the hypothesis that the bottom trawls of the shrimp vessels have destroyed the reefs mechanically. Today more than 200 German shrimpers along the North Sea coast go for the brown shrimp *Crangon crangon*. Shrimp fishery is also active in the Wadden Sea proper and is carried out with two 8 to 10 m beam trawls. Cylindrical bobbins (rollers) are attached to the ground rope. Tickler chains are not in use.

In order to elucidate the effects of the fishing gear on benthos, underwater video technique was employed (BERGHAHN & VORBERG 1993). During trawling the bobbins of the ground rope have little contact to the sea-bottom. Depending on the sediment type they jumped up and down and often float. On sandy sea-bottom the bobbins have a mean bottom contact-time of about 50%. This percentage increases when sediment becomes softer (62%), but decreases when stones or mussel shells cover the sea-floor (39%).

The rubber bobbins loose ca. 60% of their weight in water. When touching the bottom they cause little erosive effects. Penetration into sandy sea-bottom could not be demonstrated. Only the trawl shoes at each side of the beam are permanently on the sea-floor and may penetrate the bottom up to 2 cm in normal fishing operation.

In order to study the effects of a beam trawl on sabellarian reefs, an intertidal reef of *Sabellaria alveolata* at the French Atlantic coast (Island of Noirmoutier) was investigated. During high tide the reef was swept with a commercial shrimp trawl several times. Although some parts of the reef were elevated up to 1 m it was no problem for the roller armed gear to pass over it. During inspection of the swept area at low tide no damage was detectable. Only some tracks of the beam shoes were visible on the reef surface. They had crushed down the openings of the worm tubes without affecting the worms. Three days later the tubes were restored again and the tracks were no more visible. From these results it seems very unlikely that the shrimp gear has caused the decline of the sabellarian reefs along the North Sea coast.

2.3.2. Coastal engineering

The building of dikes and dams (*e.g.* connections between mainland and the islands), dredging and dumping are of great importance for the current regime. Changes in hydrological conditions may influence the above mentioned issues of larval transport, supply of nutrient and sediment as well as erosion and sedimentation. Compared to the short-term and small-scale impact of the fishery, the activities of coastal engineering cause large scale and long-term impact and can affect the whole development of a sabellarian reef.

3. CONCLUSION

Explanations for the decrease of sabellarian reefs in the German Wadden See have to consider the highly dynamic processes in a reef. Many biotic and abiotic factors act simultaneously in an unpredictable way interfered with anthropogenic effects (Fig. 2). Changes of a reef relative to size, condition, origin and disappearance can be documented, but the causes are often unknown.
A thriving sabellarian reef is resistant against its natural enemies and competitors, but will perish if larval supply fails for a longer time period. Larvae exist in the off shore area and suitable settling grounds in the Wadden Sea could be detected during the underwater video survey. Generally, the occurrence of heavy larval settlement is very rare. Throughout an investigation period of almost 10 years WILSON (1971) could observe only two heavy settlements. The absence of larvae over many years accelerates the natural development towards stagnation and destruction, but complete disappearance of a sabellarian reef is unlikely. Thus, it is well possible that there is no problem of larval supply, but a problem with larval transport. Drifting of larvae is a stochastic phenomenon and closely related to the water current regime, which can heavily be influenced by weather conditions like stormy or calm periods.

The water current regime is the only factor which is directly or indirectly effective to all stages of reef development (Fig.2). Reef origin and growth depends mainly on regularly larval settling. As mentioned above hydrographical conditions are responsible for transport and distribution of the larvae. Moreover, the water current is responsible for supply of food and tube-building material, which determines whether a reef is well-growing or stagnating. Current forces can destroy reef-buildings due to erosion or sedimentation processes. In conclusion, water current represents the most important factor to control sabellarian reefs.

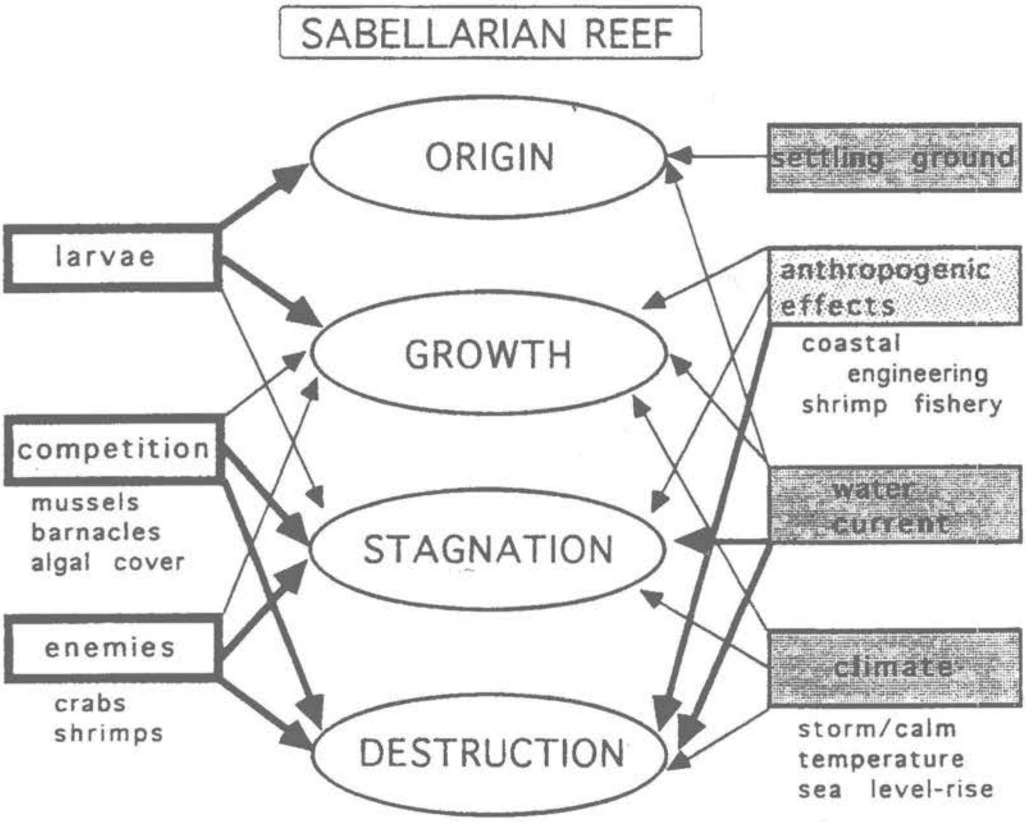

Fig. 2. Scheme of biotic (left) and abiotic (right: dark grey) factors as well as anthropogenic effects (right: light grey) which affect the natural development (middle) of a sabellarian reef. Thick arrows indicate 'direct influence' while thin arrows indicate 'indirect influence' upon the reef. Interactions between factors are not figured.

Considering the powerful water current regime the effects of shrimp fishery are negligible. In particular, the building of dikes, construction of dams, and dredging activities can change the hydrography. During the last decades many drastic changes in the Wadden Sea have been observed. In many cases they are due to the activities of coastal engineering (FARKE 1994; FÜHRBÖTER 1989; GERRITSEN 1992). Natural changes in the water current regime in the Wadden Sea are known to frequently occur, but as a slow process which is limited to a certain area. The effects of dike-building and dredging appear faster and are both large-scale and long-term. The decrease of the reefs at the German North Sea coast is regarded to be man-made since any changes in water current regime imply drastical changes for an existing sabellarian reef.

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BIOGENIC MOUND STRUCTURES IN THE PALEOCENE OF EGYPT

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Abstract - Several mound structures occur in upper Thanetian shales in the southern part of Farafra Oasis, Western Desert, Egypt. The main constituents of the mounds are worm-like tubes which stuck in the soft sediment and formed sediment-baffling frameworks. Towards the tops of the mounds, these frameworks were destroyed and the remains are broken and lying on the ground in a regularly arranged manner. Silty horizons consisting almost exclusively of tube fragments alternate with more calcareous detrital layers rich in various other bioclasts.

The shell material of the tubes (aragonite) was diagenetically dissolved. Therefore, determination of the organisms responsible for building the tubes is difficult. Some criteria suggest that the tubes had been formed by worms. However, other factors support the interpretation that the animals involved in bioconstruction belonged to the gastropod family Vermetidae.

An interpretation of the origin of these mounds is given on the basis of their inner and external architecture as well as on palaeontological and sedimentological data. A subtidal, middle to inner shelf environment with low water energy, fine clastic sedimentation and high nutrient content is assumed for the lower part. Later, when the sediment surface lay at depths with higher water energy (above storm wave base to intertidal), the mud was washed out and the fragile framework was destroyed.

1. INTRODUCTION

1.1. Location

The Western Desert covers the major part of Egypt extending west of the Nile Valley. The study area is located in the Oasis of Farafra, 400 to 500km southwest of Cairo and 300km west of Asyut. The mound structures ("vermetid debris facies" of BARTHEL & HERRMANN-DEGEN 1981) crop out in the topmost Dakhla Fm., (Paleocene), approximately 20km southeast of Abu Minqar, and about 1km east of the main oasis road where it descends from the scarp (Fig. 1, position: 27° 50' E, 26° 27' 10″ N). The thickness of the interval with the discussed mounds increases eastward and can be traced along the flank of the escarpment.

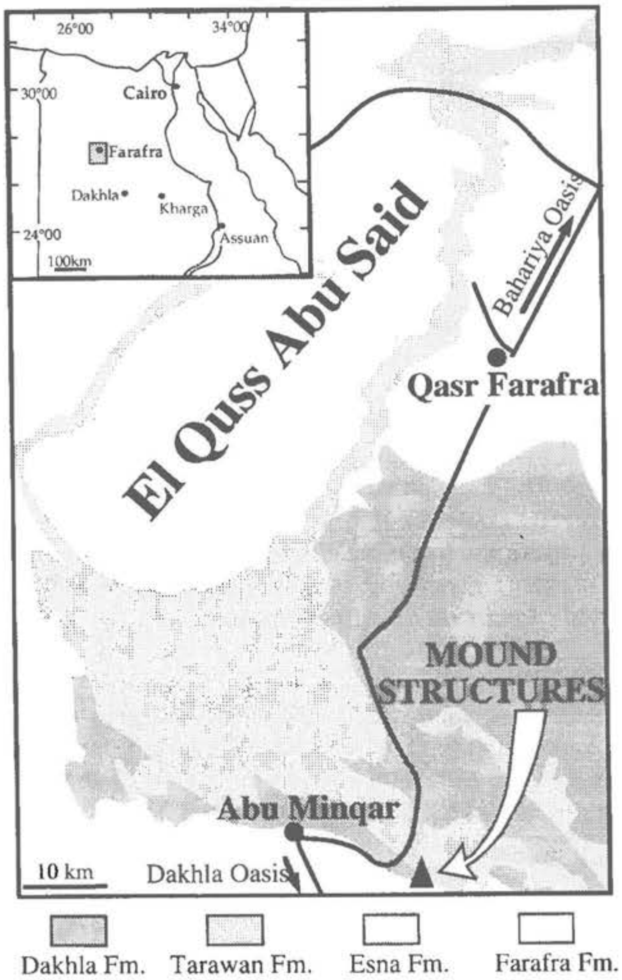

Fig. 1. Geological map of Farafra Oasis and locality of mounds.

1.2. Geological Context

The Western Desert landscape is dominated by cuestas forming plateaus with steep flanks, and wide, shallow depressions surrounded by escarpments. Rocks in the study area dip gently towards the NNE.

The deposition of uniform red and green shales of the Dakhla Fm. began in the early Danian (*Morozovella trinidadensis* Zone of BOLLI 1957) and prevailed until the Thanetian. Pelagic chalks (Tarawan Fm.) were deposited during the worldwide transgression in the upper Thanetian. In the latest Thanetian and the early Eocene shales again dominate the sedimentation. The basin was then filled, and the lithofacies changed gradually to marls and limestones of the Esna and Farafra Formations (Fig. 2).

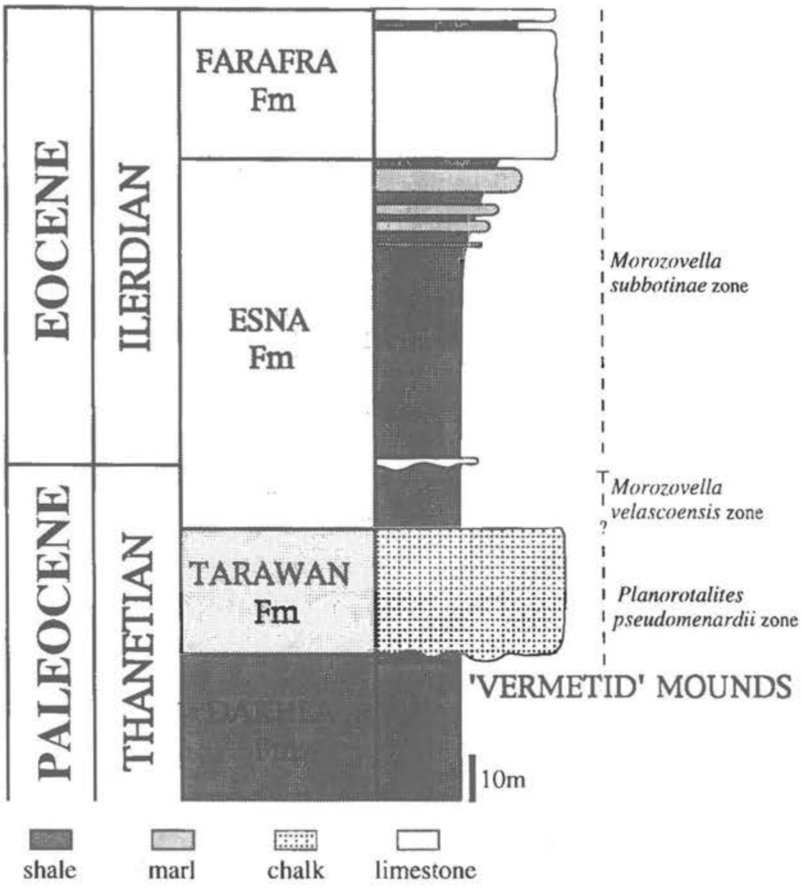

Fig. 2. Stratigraphic section of Farafra area.

The microfauna of the upper Dakhla Fm. is of a Midway-type. Similar assemblages are known, *e.g.*, from the Paleocene of Tunisia (AUBERT & BERGGREN 1976) and Libya (BERGGREN 1974). Planktonic foraminifers from samples directly below the mounds belong to the *Planorotalites pseudomenardii* Zone (upper Thanetian) of BOLLI (1957). The topmost shales of the Dakhla Fm. include two clastic layers of great areal extent suggesting tectonic activity (BARTHEL & HERRMANN-DEGEN 1981; STROUGO 1986). The "vermetid debris facies", which has the same position as these beds seems to replace these debris.

2. FACIES DESCRIPTION

Some lenticular structures occur in the shales of the topmost Dakhla Fm. near Abu Minqar, where the main road descends the cuesta of the Tarawan Fm.. Their thickness reaches a maximum of about 5m, and they extend laterally over a few tens of meters. The shales contain tubes in upright positions in the fine sediment. The tubes are at least 9cm long and about 1cm wide. Their shape is more or less rounded and longitudinally only slightly twisted. A spiral growth stage is not preserved and probably was never developed. Tapering and attachment could not be detected. The tube material is dissolved, so only steinkerns remain. Calcitic fragments in the same samples are well preserved. The tubes are believed to have originally been aragonite. The steinkerns show no ornamentation. The tubes must have had smooth inner surfaces and must have fully enclosed the soft-bodied organism that produced them.

Upsection, in the 5m bioherms, the frequency of the steinkerns increases. They are intensively intertwined, so that a framework structure is formed. A lithofacies change from shale to siltstone parallels this development. The bioconstruction apparently was able to reduce water energy and to trap and stabilise the sediment, finally leading to the formation of mounds. The outline of these bioconstructions are still preserved in their lenticular shape. They show thickening in the middle and shallow declining flanks on each side.

More and more clastic layers are intercalated with the upright growing tubes towards the top of the mounds. In more shaly horizons, the tubes are broken (Fig. 3) and regularly arranged, whereas in more calcareous levels various types of bioclasts predominate. Fragments of rhodophycean algae are the most common, but the remains of echinoids, bivalves (pectinids, oysters), bryozoans and some pellets also occur. The matrix of these rudstones is micritic, but locally may have been washed out due to episodes of higher current energy to produce grainstones. All aragonitic shell material is dissolved, and the former shape of the fragments (of the tubes and others) in thin sections is recognizable merely by micritic envelopes.

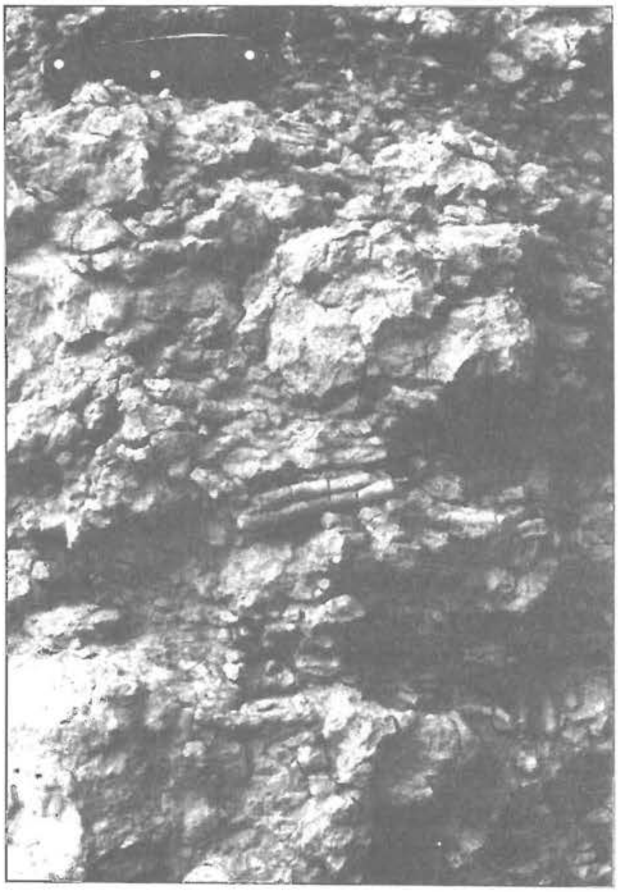

Fig. 3. Close up of broken tubes from the higher part of the mound. Knife at top of photo for scale

The surrounding sediments contain a foraminiferal fauna of planktonic and various benthic species similar to associations known from the Midway Formation in Texas (PLUMMER 1926), from the Paleocene of Libya and Tunisia (AUBERT & BERGGREN 1976; BERGGREN 1974), and the Helvetic nappes (KUHN 1992). The benthic foraminiferal assemblage is very rich, and includes species that can be taken as bathymetric indicators (AUBERT & BERGGREN 1976). To these groups belong high percentages of *Anomalinoides rubiginosus* (Cushman) and big nodosariids (KUHN 1992). Species typical for greater water depths, as well as for neritic environments are missing, which suggests that the initiation of the mounds started in a middle to inner shelf setting. At least temporarily prevailing upwelling conditions with high nutrient flux rates are indicated by frequent phosphate particles and an assemblage of nodosariids, lagenids, and some buliminids, forms that favour high nutrient input.

On top of the mounds, a hardground is formed by colonies of the oyster *Ilymatogyra osiris* (Zittel), documenting an interval of non-deposition before the transgression of micritic limestones of the Tarawan Fm..

Due to poor preservation (dissolution) it is not clear which organisms formed the tubes building the framework of the mounds. However, two groups can be considered: serpulid or sabellariid worms and vermetid gastropods.

3. MODERN WORMS AND VERMETIDS

3.1. Serpulidae and Sabellariidae

Serpulids are sessile worms (class Polychaeta) living inside bioprecipitated calcareous tubes and usually attached to a hard substratum. They filter the water for nutrition with feathered tentacles. One or two dorsal tentacles develop a chitinous or calcareous operculum to block the tube. The tubes can consist of both calcite and aragonite in specific ratios depending on the species. The sizes of the tubes range from a few millimetres up to some centimetres in length, and up to one centimetre in width. Eocene species, as described by WRIGHLEY (1951), do not reach more than 3cm in length. The tube of the Eocene *Rotularia bognoriensis* (Mantell), which has a quadrangular diameter, is the only form which can reach a length of about 8cm in its uncoiled stage. The morphology of serpulid tubes varies even within the same species, from spirally encrusting to more or less upright and free. These variations are environmentally induced, and therefore, tube morphology is a poor indicator for species determination (pers. comm. BIANCHI & MORRI 1994).

About 30 out of 300 living species are known to be able to construct framework aggregates that can reach some square metres in size. All serpulid bioconstructions occur in ecologically unstable, very shallow water environments (TEN HOVE & VAN

DEN HURK 1993). Instability includes changes in salinity, physical parameters (wave action, tides, etc.), light intensity, and temperature. It has been suggested that a high sedimentation rate of fine clastics like silt or mud prevents the formation of serpulid bioconstructions (pers. comm. BIANCHI & MORRI 1994) as none are known in calm and muddy environments.

The maximum size of the Eocene serpulid species, as described by WRIGHLEY (1951), does not match the Egyptian samples. Additionally, no mound structures constructed by serpulids have been described so far and no subtidal occurrences of serpulid colonies are known. On the other hand, we know that serpulids have great adaptability to changing ecological parameters and that their morphology varies strongly.

A closely related worm family is the Sabellariidae. The major morphological difference between serpulids and sabellariids is the missing operculum in the branchial crown of the sabellariids, so that they cannot block their tube. Only one genus of this group is known that develops a calcareous shell, all others have gelatinous, chitinous or agglutinated tubes (pers. comm BIANCHI 1994). The sabellariids occur in shallow marine environments such as intertidal to shallow subtidal with normal or schizohaline conditions. They tolerate cool water temperatures of higher latitudes, but are most common in temperate and subtropical areas (KIRTLEY & TANNER 1968). They are able to construct reefs or mound structures of which modern examples can be unlithified or only partially consolidated (BURKE *et al.* 1992; KIRTLEY & TANNER 1968; MULTER & MILLIMAN 1967). The modern examples from Belize (BURKE *et al.* 1992) are dense thickets of agglutinated worm tubes (1mm in diameter and 3cm long) capping small topographic highs (about 1m high). The surrounding sediments are muddy and sandy, and the area is protected from storm surges by a tidal shoal. The fossilisation potential of these bioconstructions and even of the sabellariids themselves is very low, but their former existence may be interpreted by the presence of circular and longitudinal ichnofossils composed of agglutinated bioclasts (BURKE *et al.* 1992).

The agglutinated tubes, as well as their dimensions, are contradictory to the material found in Egypt. No agglutinated fragments or bioclasts have been detected, although the muddy and silty sediments provide suitable components. Aragonitic tubes are very untypical in sabellarids, but the ability to build mounds in fine clastic environments protected from high currents can be taken as a modern analogous example.

3.2. Vermetidae

Vermetids are unusual growing gastropods without a spiral growth stage, closely related to the family Turritellidae. Modern vermetid snails live attached to hard substrates or to each other. Some are ciliary feeders needing agitated water for their feeding mechanism, whereas others, such as *Vermetus gigas*, use mucous strings to filter the water and thus are adapted to calm water without strong currents. Their shells are composed only of aragonite. Shell dimensions vary from species to species, but may reach considerable lengths and diameters. Shell morphology is variable, and causes much confusion even in the study of modern vermetids. Modern vermetid "banks" are well-known from intertidal, subtropical environments (SAFRIEL 1974; HUGHES 1979) where they are often accompanied by red algae. Fossil examples as described, *e.g.* by LABOREL (1980), are thus taken as precise palaeo sea-level indicators. Several algal-vermetid reefs are known from the Miocene (Badenian), *e.g.* in Poland (PISERA 1985; KRACH 1981) and Moldavia (JANAKEVITSCH 1977). The vermetid facies from Poland is interpreted to be of shallow water origin, and grews on topographic highs on the underlying Cretaceous sediments. These reefs pass laterally into sands and grainstones with various bioclasts and locally intercalated oyster bioherms (PISERA 1985).

Vermetid-like gastropods are known from the Red Sea, that as regularly growing juveniles stick in the muddy sediment. In the adult stage, they stretch the tubes upright and free into the water column (pers. comm. HOTTINGER 1994). Their tubes are not attached to each other, but are often intertwined. Their shapes and sizes are very similar to the steinkerns from Egypt. They show no ornamentation on the inner surface of the aragonitic wall, which is very thin (about 1mm) compared to its length of about 10 to 12cm. All along these tubes a conspicuous open slit is developed. These gastropods live in groups in water depths of about 100m and cover areas of about 1m^2. The environment is normal marine and only low water energy prevails. The open slit indicates that they belong to the gastropod genus *Siliquaria*, which belongs to the family Turritellidae.

The exclusively aragonitic tubes of vermetids, their tube morphology without regular coiling and tube dimensions fit well to the described fossil remains from Egypt. The existence of vermetid banks in intertidal settings where very strong currents and surges are likely is, on the other hand, not a good modern example for the probable palaeosituation in which the Egyptian mounds were formed. The ecological context of the siliquariid gastropod colonies in the Red Sea and life-conditions as partly mud-sticking organisms give a much better idea of the fossil example. As siliquariids, in contrast to vermetids, do have a regularly coiled endobenthic first growth stage, it is unlikely that the remains from Egypt belong to this genus. Although the fossilisation potential of infaunal organisms or infaunal parts of organisms is much better than of tubes erected above the seafloor, no regularly coiled shells have been found in the field. Nevertheless, both genera are very closely related and it seems possible that vermetids could also have lived as mud stickers as do silliquariids today.

5. DISCUSSION

BARTHEL & HERRMANN-DEGEN (1981) gave a short description of the discussed buildups as "vermetid debris facies indicating a fan marginal to an uplifting area". In my opinion, this interpretation has to be reconsidered.

The environment in which the mounds grew is well characterized by microfaunal and sedimentological data (see chapter 2). Deposition first occurred in a low-energy, subtidal environment of the middle to inner shelf, probably below storm wave base. The framework formed by upright growing animals was able to baffle and stabilise the sediment, and therefore, supported the formation of an elevated mound (although this does not mean that it was very high above the sediment surface). With increasing water energy due to the filling of the basin, the sediment was washed out and the framework destroyed. This shallowing may have been due to a simultaneous sea level fall, denoted by the sequence stratigraphic context; also tectonic disturbances may have occurred (BARTHEL & HERRMANN-DEGEN 1981; STROUGO 1986). My data suggest that mound formation was the result of increased sediment accumulation because of baffling and stabilisation. This, like a positive feedback mechanism, added to the further density of population. After destruction of parts of the mounds, resedimentation is suggested to have been autochthonous, and occurred more or less where the mound was built. This interpretation is strengthened by the fact that no tube fragments could be found in shale samples lateral to the mounds.

The origin of the tubes remains unclear. Mass occurrences of tubes forming a framework are known from both worms (above all, serpulids) and gastropods, even though exclusively from intertidal settings and not in such dimensions. Serpulids, which are important framework builders, may have aragonitic tubes, but their tubes are too small and no serpulid colonies are known from muddy, low-energy environments. Sabellariid worms and siliquariid gastropods are further candidates, because both can live as mud-stickers. Sabellariids, however, are agglutinators and very small. Siliquariids have big aragonitic tests, but have an endobenthic spiral growth stage which was not detected in the Egyptian fossil examples.

In my opinion, vermetids are the best candidates as mound constructors for the Egyptian mounds. Vermetid tubes are aragonitic, have the right size, do not develop a spiral growth stage, but have a twisted and unregularly coiled tube. It seems very probable that vermetids are able to live as mud-stickers in low-energy environments comparable to their closest living relatives: the siliquariids show this habit during adolescence, and the turritellids live their whole life as endobenthos in fine sediment.

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INCIPIENT STROMATOLITE/BRYOZOAN/SERPULITE REEFS IN A MEDITERRANEAN LAGOON NEAR NARBONNE (FRANCE)

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Abstract - Stromatolite limestone crusts develop underneath algal mats on pebbles in the brackish lagoon, Lac d'Evêque, southeast of Gruissan (Aude), France. In the same lagoon, small bioherms of serpulids, and the bryozoan *Electra* are found. Such associations have built reefs from the lower Carboniferous onward, always in marginally marine situations under shallow hypo- or hypersaline water. The same organisms as in Gruissan constructed massive bioherms along the Miocene coast of the Paratethys in Poland and Russia. Presently, *Electra* and stromatolite build up reeflike limestone bodies in brackish inland waters of the SW Netherlands - because of climatic factors, the serpulids cannot thrive there. The Dutch localities are artificially dammed erosion gullies, filled with oligohaline water not loaded with sediment. The Mediterranean locality has a very low relief, and ecological gradients are faint. This keeps the potential reef-builders spatially isolated. It is surmised that stromatolite/serpulite/bryozoan reefs will develop along Mediterranean coasts as soon as favourable conditions (varied lagoon bottom topography, rise of brackish water level, decrease of clastic influx) arise.

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GROWTH HISTORY OF A MODERN ALGAL RIDGE/STROMATOLITE FRINGING REEF, STOCKING ISLAND, BAHAMAS

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Abstract - The growth history of an algal ridge/stromatolite reef complex off Stocking Island in the Exuma Cays, Bahamas, has been reconstructed from eight cores and fourteen radiocarbon dates plotted in relation to a Bahamian sea-level curve. This reef is up to 2.1 m thick, is established on a Pleistocene terrace, and appears to be best developed off the central section of Stocking Island, where it is about 50 m wide and can be divided into three distinct surface zones:
(1) The back reef and reef flat consist of a **stromatolite zone** characterized by unlithified to lithified mats of fine sand bound by the cyanobacteria *Schizothrix*.
(2) **A coralline/ *Echinometra* zone** occurs seaward of the stromatolites. This zone is extensively eroded by the urchin *Echinometra lucunter,* and most surfaces are covered by algal turf and macroalgae. Branching *Neogoniolithon strictum* is common, particularly at the inner limits of this zone, and scattered coral colonies occur along its outer limits.
(3) **A pinnacle zone** occurs at the seaward limit of the fringing reef; in this zone the sea floor drops to a depth of 4 m and numerous pinnacles and ridges rise from the smooth, sand-swept rocky floor. Most pinnacles have smooth surfaces, but some are covered with rough crustose coralline caps and growths of macro-algae.

Subsurface data from cores indicate that the Pleistocene limestone terrace is composed of a well-sorted fine to medium calcarenite containing root casts and caliche crusts. The Holocene sections above this terrace consist of four reef facies-vermetid limestone, *Neogoniolithon* limestone, stromatolite, and calcarenite.

The reef complex was apparently established about 4,500 years B.P., beginning as an intertidal vermetid buildup on a Pleistocene limestone terrace. With the flooding of the terrace about 4,000 years B.P., the branching and sediment-tolerant coralline *Neogoniolithon strictum* became dominant, overgrowing the vermetid facies, and constructed a ridge at the outer edge of the terrace. The *Neogoniolithon* ridge caught up with sea level about 1,500 years B.P., forming a raised intertidal lip. Wave-energy conditions were reduced on the leeward side of this elevated lip allowing shifting sands to accumulate in the back-reef lagoon. Few reef organisms were able to settle in this inshore sediment-stressed environment, but sediment-trapping cyanobacteria flourished and formed stromatolites. When offshore wave-energy conditions were reduced about 500 years B.P., possibly associated with growth of a bank-barrier reef, the algal ridge was invaded by the urchin *Echinometra lucunter*, which eroded this ridge and reduced its relief. This urchin is now starting to destroy the seaward edge of the stromatolite buildups. Today active stromatolite accumulation is taking place only in back-reef areas adjacent to shifting beach sands.

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ENCRUSTATION PATTERNS ON LOWER MIOCENE MACROFOSSILS AS AN EXAMPLE FOR NON-ANTHOZOAN REEF CONSTRUCTION

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Abstract - Macrofossils of the Lower Miocene Zogelsdorf Formation from the Austrian Paratethys are often partially or wholly encrusted by diverse organisms including bryozoans, barnacles, serpulids and red algae. These components also dominate a number of facies within the limestones making up the formation. Complicated encrustation patterns and sequences are especially found on specimens of the irregular echinoids *Echinolampas* and *Clypeaster*. These were investigated as far as taxonomic presence, % coverage, direction of growth, and space competition of epibionts are concerned. The methodology used consists of mapping the presence and composition of the taxa using an image analysis program.

The stability of the substratum is known to be a major factor in the distribution and frequency of epibiont presence. This data suggest a sustained residual surface time for the echinoids which represent relatively large stable substrates in an otherwise unstable environment. This is supported by recent observations on encrusted irregular echinoids from the Northern Adriatic which are found to quickly become covered by epibionts upon death if exposed at the sediment surface. These can be seen as an example of non-anthozoan reef constructions as they represent topographic elevation above the sediment surface, as well as sites of both complex biological interactions and sustained carbonate production. Although operating on a comparatively small scale, an understanding of the complex, interactive processes involved in the construction of these encrusting sequences can be relevant for the interpretation of larger scale reef structures.

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MICROBE - LITHISTID SPONGE ASSOCIATIONS IN LATE LUDLOW (SILURIAN) MUDMOUNDS OF THE DOURO FORMATION, CANADIAN ARCTIC ARCHIPELAGO

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Abstract - Carbonate buildups on southwestern Devon Island and southern Ellesmere Island are part of an extensive reef province that can be traced through the Arctic Islands and perhaps extending into the Urals. Three main types of buildups are recognized: 1) mudmounds, 2) coral-skeletal mounds, and 3) coral-stromatoporoidskeletal mounds. The skeletal mounds have mudmound cores and show a biological zonation from mudmound cores to a coral facies and terminal coral-stromatoporoid facies that represent an overall shallowing upward succession. Cores of the skeletal mounds are extensively dolomitized and show relict micrite fabrics. The better preserved mudmounds have sponge spicules and micrite fabrics of probable microbial origin, they average 50m in width and 15m in height. They are elongate NW - SE, probably indicating prevailing current directions. Solitary and colonial rugose corals, stromatoporoids, trilobites, brachiopods, crinoidal debris, and rare lithistid sponges characterize mudmound flank facies.

Small (0.5m high x 3m wide), well-preserved mudmounds, exposed near the base of one of the larger mudmounds in the study area, provide information concerning the initial development of the diagenetically altered mudmounds and skeletal mounds. Lithistid sponges, microbes and dasycladacean algae formed an intricate association of binders, bafflers and encrusters within the small mudmounds. Relict fabrics in the larger, more diagenetically altered mudmounds and skeletal mounds suggest the presence of this biota.

The mounds occur at a level of substantial platform drowning that resulted in the onlap of basinal shales of the Devon Island Formation onto the Douro ramp carbonates. A conspicuous hardground at the formational boundary caps several of the mudmounds and reflects a hiatus in deposition during deepening which resulted in the termination of mudmound development.

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MICRITE PRODUCTION AND HILL STABILISATION BY MICROBIAL COLONIES - A CASE STUDY FROM A FRASNIAN MUD MOUND

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Abstract - An interesting mud mound with typical properties has been identified in Upper Devonian (Mid-Frasnian) reef debris limestones of the Elbingerode Complex in the Harz Mountains. It is named after the village of Rübeland south of Elbingerode.

Mud-mounds are small, hillshaped limestone-buildups of pure micrite with steep flanks (20 to 40°), accumulated in a marine subtidal environment. Any rigid framework of corals or other baffling organisms is absent. They are rich in stromatactis, bear often zebra-limestones and bindstone mats. Macrofossils are rare, beside scattered sponges. The source of micrite and the stabilisation of the slope were enigmatic in the past. Recently, an essential participation of microbial colonies, has

become more and more evident, after my first assumptions in the late eighties were without evidences.

The Rübeland mud mound contains all the named properties. It consists of a stromatactis-bearing micritic matrix of white mudstones and black microfossiliferous wackestones. Intercalated are some layers of zebra-limestones and a special kind of stromatolite, not yet known from other mud mounds. As well in the matrix as in the zebra layers, there are constituents interpreted formerly as being of microbial nature. The stromatolites were exclusively explained as early cemented metabolic products of micrite formed by microbial colonies.

Meanwhile it was possible to find numerous evidences for a microbial formation of micrite to verify the assumptions:

1. In all components of the mud mound there are layers with coccoid cyanobacteria (tiny ellipsoids and rods, surrounded by a thin seam of calcite - the former glycocalix): on top of the stromatolitic laminae, in some matrix lumps, in calcite mats of zebra layers.

2. The bulk of stromatolitic laminae consists completely of a very fine and dense network of filaments (cyanobacteria); they are assumed to be the producer of the stromatolites.

3. The white mudstones of the matrix show in thin sections a distinct thrombolitic structure, mostly moderate compacted: tiny, erect, micritised bunches are surrounded by calcite seams (post-mortem-cement fringe) forming together cm-sized patches. All the light mudstones, corresponding to about 50% of the whole matrix, are of identical type and entirely formed by microbial colonies of the group *Angulocellularia* or *Epiphyton*.

As a consequence, one can conclude, that all stromatolites, all white constituents of the matrix and some parts of the zebra limestones are of microbial origin. The cyanobacterial colonies are interpreted to have produced the micrite, which was deposited in situ within the slimy jelly mats. Therefore, more than 50% of the whole mud mound is produced by microbes.

The immense amount of jelly colonies seems to be the main factor for hill stabilisation together with an early biocementation. A rigid framework was not necessary.

ECOLOGY OF RECENT AND FOSSIL REEF ORGANISMS

AUTECOLOGICAL CASE STUDY OF LATE JURASSIC *Thamnasteria* (SCLERACTINIA) SPECIES WITH SMALL CORALLITES

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Abstract - Independent of their occurrence in or outside reefs, species of the scleractinian *Thamnasteria* with small corallites show a very high morphological plasticity by their foliose, massive, encrusting or ramose growth. These variations are mostly due to a response to different hydrodynamic and sedimentological conditions. Other criteria relevant for an autecological analysis are grouped as primary (morphology, orientation of corallites, colony base, corallite characters) and secondary (sedimentological characteristics of the matrix) data. Together with dominance and diversity patterns these findings indicate a general tolerance of broadly varying ecological factors, so that at least *Thamnasteria concinna* (Goldfuss) may be called euryoecous. In northern Germany, its optimum is reached in turbulent environments with low sedimentation rates, however.

1. INTRODUCTION

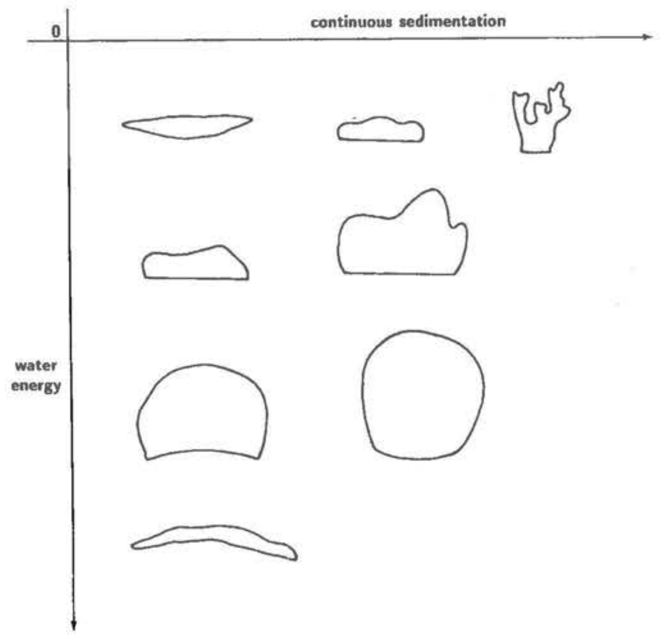
Fossil scleractinians are treated extensively in the literature but very few papers deal with the ecology of individual taxa. In the Upper Jurassic in northern Germany, fourteen localities yielded corals from the Oxfordian and Kimmeridgian (for details on sampling and localities see BERTLING 1993a; b). Because various facies types are represented, autecological demands can be well delimited by a comparison of different environments. Further information with a detailed discussion of facies parameters has been published elsewhere (BERTLING 1993a; b). *Thamnasteria concinna* (Goldfuss) is the most frequent and ubiquitous element here.

The taxonomic status of the species has been considered by RONIEWICZ (1982) and BERTLING (1993a). It has become clear that at least some specimens formerly determined as "*Thamnasteria gracilis*" (Münster) belong to *T. concinna*. On the other hand, it can not be definitely excluded that more than one (homoeomorphous) taxon is represented by *T. concinna* as in current usage. Contrary to the author's previous opinion, there might be biologically distinct species with differences in physiology. This could be expressed by minute differences in corallite size (RONIEWICZ 1994, pers. comm.). However, the sibling species then would show an almost identical reaction to varying ecological factors, as has been demonstrated for the Recent *Montastraea* (BUDD 1993).

Despite strongest similarities in linear measurements such as corallite arrangement and size, *Thamnasteria dendroidea* (Lamouroux) has a growth rate about ten times higher and shows unique morphologies not shared by *T. concinna*. Because the occurrences of the two taxa seem to be mutually exclusive, however, they might be ecomorphs of a single biological species.

2. AUTECOLOGY OF *Thamnasteria concinna* (Goldfuss)

The ecological investigation of fossil corals mostly relies on their general morphology. However, other items may be regarded as primary data as well: the skeletal growth is also connected to the orientation of the corallites, the type of corallites, and special features of the growth history. Other criteria, mainly of sedimentological character, may be considered as secondary data. They comprise mostly the grain size of the matrix and the microfacies (*e.g.* cement, texture) in which various specimens occur.



Morphological variation of
Thamnasteria concinna (GOLDFUSS)

Fig. 1. Morphological variability of *Thamnasteria* species with small corallites as related to intensity of continuous sedimentation and water energy (according to data of RONIEWICZ & RONIEWICZ 1971; BEAUVAIS *et al.* 1974; TURNŠEK & MIHAJLOVIĆ 1975; LATHUILIÈRE 1984; RONIEWICZ 1984; LEINFELDER 1986; and own results).

2.1. General morphology of the corallum

The colony form of *Thamnasteria* species with small corallites from various localities all over Europe shows a very high variability (Fig. 1). One of the prominent ecofactors governing the morphology is water energy. In Upper Jurassic rocks of northern Germany, platelike coralla come from localities whose sediments indicate calm, turbid positions, whereas head-shaped types are typical of localities sedimentologically characterized as turbulent, shallow marine environments. In extremely agitated water, the thickness of the colonies diminishes again, leading to flat, encrusting types. This means that the degree of corallum convexity alone (i.e. the thickness of the coralla) is a good indicator of water energy (see also RONIEWICZ & RONIEWICZ 1971; LATHUILIÈRE 1984 and LEINFELDER 1986).

In addition, *T. concinna* shows corallum variation based on its responses to rates and intensity of continuous sedimentation, as has been claimed before for Recent scleractinians (*e.g.* FAURE 1974; WIJSMAN-BEST 1974; BOREL-BEST *et al.* 1984; STAFFORD-SMITH 1983). Corals in the northern German Late Jurassic sea grew under mostly low net-sedimentation rates leading to a prevalence of simple morphologies. Elsewhere, more elevated forms tending towards ramose morphology grew in calm water with strong influx of fine clastics (TURNŠEK & MIHAJLOVIĆ 1973; BEAUVAIS *et al.* 1974), and rounded growth also indicates turbulent environments under high sedimentation rates. Thus, the role of continuous sedimentation for corallum morphology was more important at low water energies.

Intermittent sedimentation (*e.g.* by storms) did not produce these types of coralla because *T. concinna* obviously was adapted to the ``normal" conditions prevailing at its habitat. This means that storm effects (as obvious from sedimentology) were more severe for colonies living in deeper than for the ones in shallow-water facies: even a thin layer of sediment deposited on the surface of a flat corallum grown in calm water may have suffocated numerous polyps.

The role of light in inducing changes in the corallum morphology (MACINTYRE & SMITH 1974; GRAUS & MACINTYRE 1976) of fossil corals is difficult to assess but it may be equated with the presence or absence of symbiotic zooxanthellae. Investigations of stable isotopes in knobby colonies of *T. concinna* from Poland have advocated a non-zooxanthellate status of the coral (GRUSZCZYNSKI *et al.* 1990; STANLEY & SWART 1995), differing from author's previous assumptions (BERTLING 1993b). However, it remains to be demonstrated that all representatives of the species (group) lack zooxanthellae: the increased growth rate by a factor of ten, respectively, of *Thamnasteria dendroidea* (Lamouroux) suggests the presence of the symbionts in this case.

2.2. Orientation of corallites and growth history

The form of coralla is directly connected to the growth directions of corallites. Radial orientation results in head-shaped colonies, linear growth upward produces plate shapes once the corallites have terminated their incipient sideward growth (MACINTYRE & SMITH 1974). If *T. concinna* was a non-zooxanthellate coral, then the orientation of corallites must be related to processes exclusive of exposure and photoperiod. It may be speculated about an orientation toward a food source but this issue can not be solved palaeontologically. On the other hand, sedimentological control is obvious.

The shape of the colony base directly reflects the net-sedimentation rate during its young stages (PHILCOX 1971): coralla which have flat or concave bases started growing unhampered, whereas conical or strongly convex bases can only be explained by the necessity to cope with strong sedimentation. This is the case especially in microfacial types indicating calm-water where colonies frequently also show constrictions caused by partial mortality. After sediment covered lateral polyps, *T. concinna* reacted by strong sideward growth of the unaffected areas. This led to the recolonisation of the substrate and finally to the reunification of formerly dissociated parts of the same colony. Toppling by turbulent conditions in shallow water was much better tolerated, since the species continued to grow under directional changes of 90° - 180°.

A good record of the growth history is kept as seasonal banding which is directly visible on many specimens because of neomorphous sparitisation. These growth bands are only 1 to 2 mm thick; similar values were recorded from corals in the English Oxfordian (ALI 1984) but most Recent hermatypic corals grow much faster (review in DAVIES 1983). The generally low growth rates do not necessarily have to be attributed to lacking zooxanthellae because *T. concinna* produces a very dense skeleton thus depositing comparable amounts of calcium carbonate as Recent hermatypes (ALI 1984). Also, turbidity strongly hampers calcification in zooxanthellate corals (GRAUS & MACINTYRE 1976; CORTÉS & RISK 1985), thereby reducing growth rates. Besides age determination of some colonies as 60 - 120 years old, seasonal layers provide evidence of varying environmental factors, caused by a climate with marked seasons.

2.3. Corallite characters

Due to the highly variable length of their confluent septa, calices of *T. concinna* may be arranged in different ways: either in parallel rows or in equal distances. This plasticity in growth together with an increased budding rate after coverage with sediment was essential for the successful recolonisation of lost areas mentioned above. The coral obviously reacted to confined or open space in the adjacent areas; extreme forms of corallite spacing repeatedly occur together on the same surface of single knobby or head-shaped coralla (BERTLING 1993a). The former distinction of different species on this basis alone can thus no longer be valid, especially since this variability is not size-dependant. However, it has been proposed (BUDD 1993, BUDD *et al.* 1994) that intracolonial and intercolonial variation can only be separated from interspecific variation by multivariate statistics. This would require perfectly three-dimensionally preserved corallites without any abrasion or diagenetic alteration. As a consequence, most fossil corals would prove to be unidentifiable at the species level. The transferability of her results has been questioned by BUDD (1993) herself, and phaenotypic patterns in other genera may be completely different (see *e.g.* BOREL-BEST *et al.* 1984).

The size and depth profile of calices as well as their septal numbers are important for the potential of polyps to remove sediment from their surface (HUBBARD & POCOCK 1972; WIJSMAN-BEST 1974; STAFFORD-SMITH 1993). According to its calice characteristics *T. concinna* must have been very inefficient at active sediment removal. More important than corallite morphology, however, may be the polyps' cleaning behaviour and passive effects related to corallum morphology; in any case fine sediment is removed faster than the coarse fraction (BAK & ELGERSHUIZEN

1976; LASKER 1980; STAFFORD-SMITH 1993). The knobby morphology of *T. concinna* with deep valleys between the knobs to act as transport furrows thus strongly eased growth in occasionally storm-affected environments (RONIEWICZ 1984). Corals with low potential to reject sediment mostly tolerate several days of coverage (STAFFORD-SMITH 1993), thus compensating their disadvantage due to reduced metabolic rates (LASKER 1980; CORTÉS & RISK 1985) to some extent. It can only be speculated about the conditions in *T. concinna* regarding these questions.

2.4. Secondary Data

The grain size of the enclosing matrix contains additional information. In the northern German Upper Jurassic, *T. concinna* is rare in marly limestones with micrite cements. Instead, it occurs frequently in coarse-grained biogenic limestones. Cement and grain-size of the host rocks of the coral thus point in the same direction: high-energy environments in the Late Jurassic German sea were more suitable than calmer waters with higher sedimentation rates. However, this finding contrasts with the opposite situation in southern Poland (RONIEWICZ & RONIEWICZ 1971).

2.5. Summary of autecology of *Thamnasteria concinna* (Goldfuss)

In various ways *T. concinna* coped effectively with different environments. High net-sedimentation rates were problematic for a poor sediment remover like this coral. As a consequence, it frequently suffered partial mortality. Even ramose coralla could not develop under strong continuous sedimentation since the species could not grow upward fast enough to attain a reasonable height. Moderate sedimentation rates favoured the ramose growth type, however. In turbulent water, *T. concinna* formed compact heads; besides their resistance to turbulence, sediment grains fell off their surface very easily. That is why partial mortality due to smothering is hardly ever recorded in these colonies. Toppling occurred more frequently, but *T. concinna* easily managed directional growth changes. For this reason, the species preferred turbulent water with low net-sedimentation rates in Germany. It was only able to survive in other environments because of its high morphological plasticity.

3. SYNECOLOGICAL IMPLICATIONS

The functional significance of *T. concinna* within the coral associations varied with its changing morphology. In northern Germany, head-shaped colonies could act as reef builders by establishing a rigid structure of closely neighboured "boulders" in an unstable surrounding. Plate-like coralla only functioned as binders of loose fine-grained sediment by overgrowing it together with older (*i.e.* dead) colonies of similar shape. Hence, net-sedimentation rates also influenced the synecological function of the coral associations via the colony form of *T. concinna.*

A quantitative study in northern Germany yielded the ubiquitous and euryoecous *T. concinna* to be the dominant element at the numerous localities sedimentologically characterized by low net-sedimentation rates and strong water movement (BERTLING 1993b). This is explained by the species' variability in the arrangement of corallites. Similar results were obtained by RONIEWICZ (1984) for a locality in the Polish Oxfordian and may also be concluded from the extensive literature. If the taxonomic identifications of numerous previous authors are correct (see references in BERTLING 1993b), *T. concinna* only had reduced importance at the Central and West European deeper water localities where corals (*e.g. Microsolena, Isastrea*) with larger and stronger ornamented calices and thus better sediment rejection capabilities prevailed.

The strong dominance of few taxa at each locality is generally typical of communities in a stressful environment. In this situation diversity indexes are always low (*e.g.* KÜHLMANN 1974; CORTÉS & RISK 1985) which can also be demonstrated for northern Germany. Any taxon dominant in this facies has to be well adapted to locally varying environmental factors. Thus, *T. concinna* sometimes seems to have been at least abundant in pioneer stages of reef development in Central Europe (*e.g.* PAULSEN 1964; RONIEWICZ & RONIEWICZ 1971).

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DYNAMICS AND LIMITATIONS OF HERBIVORE POPULATIONS ON A CARIBBEAN CORAL REEF

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Abstract - To evaluate the hypothesis that herbivore populations are limited by food supply, a quantitative description of primary production and consumption was made for one study site in the Caribbean (Bonaire, Netherlands Antilles). Primary production (kg C/ha/day) on the shallow reef was calculated from irradiation of PAR at 2 m depth, P-I curves that were determined for the main algal food types, and their percentage cover. Daily consumption of algal C (kg C/ha/day) by reef herbivores was calculated from their density and their mass-specific food intake. Density (ind/ha) and biomass (kg/ha) of herbivorous fish and sea urchins were monitored by repeated visual surveys in a permanent transect, and the relationship between fish wet wt (FWW) and daily consumption of algal C (consumption = 0.0342 $FWW^{0.816}$) was obtained using published data on herbivorous coral reef fish. Annual mean production was 17.2 kg C/ha/day, with winter minima of 14.6 kg C/ha/day and summer maxima of 18.6 kg C/ha/day. Averaged over all census intervals, all algal production on the shallow reef was directly consumed, almost entirely by fish. Primary consumption varied with season (winter: 14.1 kg C/ha/day; summer: 20.8 kg C/ha/day), closely following the available production. The seasonal variation in consumption is caused primarily by lower fish densities on the shallow reef in winter when fish move to deeper reef parts. It is concluded that food supply is presently limiting the size of herbivore populations on the shallow reef. *Diadema* mass mortality caused a sudden increase in food supply for herbivorous fish > 5 years prior to the onset of the study. It is argued that, following this disturbance, changes in the abundance of functional groups of herbivores have followed a predictable pattern of succession, driven by competition for food resources.

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ECOLOGICAL IMPLICATIONS OF PALYTOXIN IN THE CORAL REEF

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Abstract - Toxicity is a widespread phenomenon in coral reef organisms. The high incidence of highly toxic forms seems to be an evolutionary response to their uniform and stable environment and to the typical characteristics of coral reefs such as the limiting factor of living space or high species diversity.

Zoanthids of the genus *Palythoa*, which are often abundant on tropical shores and coral reefs, have been shown to produce the apparently most powerful marine toxin (Palytoxin). However, recent studies in the region of Santa Marta at the Caribbean coast of Colombia, indicate the occurrence of palytoxin not only in the two investigated *Palythoa* species but also in two other zoanthid species of the genus *Zoanthus*.

Although higher toxin concentrations are found in fertile polyps, it is unlikely that palytoxin production is significantly correlated with the reproductive cycle of the zoanthids. Higher concentrations may be mainly due to larger mass of organs and eggs where the toxin is easily adsorbed. The toxin also was found in one *Palythoa* species that always had been sterile during the investigation time.

Palytoxin has been identified in other invertebrates such as in the crustacean *Platypodiella spectabilis,* which lives under the crust of *Palythoa* colonies, and in the polychaete *Hermodice carunculata,* which feeds on zoanthids. Moreover, several reef fishes (*Chaetodon* sp.) prey on these crustaceans and on the zoanthids as well. This indicates that the toxin may be easily sequestered to other marine organisms and may accumulate via the food chain. Its occurrence in ciguatera fish poisoning has also been suggested.

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SEXUAL AND VEGETATIVE REPRODUCTION OF THE SOFT CORAL *Sarcophyton elegans*, LIZARD ISLAND, NORTHERN GREAT BARRIER REEF

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Abstract - During three years reproduction in the octocoral *Sarcophyton elegans* was studied in the lagoon at Lizard Island, northern GBR. *S. elegans* is a dioecious species with gonads in the autozooids. The eggs have a biannual developmental cycle, but oogenesis occurs every year. The sperms develop in ten months. The colonies have a size of > 15 cm basal circumference at first reproduction. The ripe eggs have a diameter of 450 - 700μm. Colonies of *S. elegans* release their eggs from the edges of the colonies during two nights, six days after full moon in September, and during subsequent months the gametes are released in a circular pattern closer to the centre for each broadcast spawning. The peak of gamete release synchronises with the annual mass spawning event in December. In 1991/92, 1992/93 and in 1993/94 all the gametes were released before February.

The sex ratio males:females is 1,3:1. The species reproduce asexually by fission and budding, with a slightly higher rate of buddying in males. This can explain the skewed sex ratio.

This study showed that one large assemblage of *S. elegans* contained both male and female colonies, suggesting that more than one clone is present. I used allozyme electrophoresis to identify the clones, and found a surprising abundance of clones. This shows that sexual reproduction in the species is more prevailing than previously thought.

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INFLUENCE OF BATHYMETRIC AND SEASONAL CHANGES ON THE PRIMARY PRODUCTIVITY OF DIFFERENT CORAL SPECIES, IN THE GULF OF AQABA, (JORDAN)

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Abstract - The experimental area, the Gulf of Aqaba belongs to the northern boundary of the existence of photic tropical/subtropical reefs. The rate of photosynthesis as well as the photosynthetic efficiency of whole coral colonies in situ, small pieces of colonies in vivo and of freshly isolated

zooxanthellae in vitro as a function of photon flux density was investigated. The samples were collected along a vertical transect, SSW orientated in front of the Marine Science Station Aqaba. To get an idea about the natural light-conditions, the photon-flux-density was registrated weekly over a period of two years along this transect.

Phototrophic energy-sources
The experiments for the photosynthetic productivity of complete coral colonies and small pieces of colonies were performed with four species (*Acropora variabilis, Acropora squarrosa, Stylophora pistillata* and *Mycedium elephantotus)* collected in 5, 10, 20 and 40 m depth. The zooxanthellae were prepared from *Mycedium elephantotus*, also collected in depths from 5 to 40 m. For the experiments with small coral pieces, tips of branched corals were cut off and glued to small plastic cylinders. These nubbins were brought back to the original growing depths for two weeks, before the measurements were done. For the isolation of the zooxanthellae the tissue was removed from the skeleton with an "Airbrush System". The zooxanthellae were separated from the tissue homogenat over Percoll-gradients, basically according to the method of TYTLER & SPENCER-DAVIES, 1983. The experiments with isolated zooxanthellae and nubbins were carried out in temperated respiration chambers with a variable volume between 0,5 and 3 ml. Data were logged on a PC data base.

The values for the compensation points, the maximum photosynthetic-rates (Pmax) and the photosynthetic-efficiencies (α) were higher for whole colonies compared to isolated zooxanthellae. The Pmax-rates of whole colonies were independent from the growing depth, nearly five times higher than those of isolated zooxanthellae from the corresponding depths. The measurements with zooxanthellae from *M. elephantotus* indicate, that these corals reach their upper distribution limit at a depth of five meters. Additionally to the measurements of photosynthetic parameters, from each probe aliquots were taken for the determination of the amount of zooxanthellae, the pigment content and the protein-concentration as baselines to standardise the metabolic data.

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A SYMBIOSIS BETWEEN THE SCLERACTINIAN CORAL *Calamophylliopsis* AND A POLYCHAETE (TITHONIAN-BERRIASIAN)

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Abstract - Symbiosis includes various types of associations between different organisms (*e.g.* mutualism, commensalism, parasitism). Corals are important hosts for a great diversity of specialised symbionts. Surprisingly few instances of macrosymbionts intergrown with scleractinian corals have been described from Mesozoic.

An unknown example of a coral-polychaete intergrowth symbiosis has been recognized in exotic boulders of the Stramberk-type limestone (Tithonian-Lower Berriasian, Polish Outer Carpathians). Tubes, interpreted as polychaetes, have been identified within calices for 3 of 7 phaceloid colonies of *Calamophylliopsis flabellum* (Michelin, 1843) (Dermosmiliidae, Astraeoina). Some tubes are also attached to the outer side of the coral skeleton. In one colony all individuals appear to be infested, in two others, tubes have been identified only in some individuals. Tubes, usually 1-4 per calice, are ca. 0.5-1 mm in diameter. The position of most tubes within calices is straight upright or oblique, but some of them are curved showing a U-shaped pattern. Modification of the coral skeleton by polychaetes and position of the tubes indicate that polychaetes grew contemporaneously with polyps. It is likely that polychaetes encrusted corallites and then penetrated into gastric cavities of polyps. The

character of the described symbiotic association can be only subject of speculation. Polychaetes could profit from the coral by obtaining a place to live, food or protection. It is possible that this association was not detrimental for the coral.

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INFLUENCE OF BATHYMETRY AND SEASONAL CHANGES ON THE CARBONATE DEPOSITION OF DIFFERENT CORAL SPECIES IN THE GULF OF AQABA, (JORDAN)

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Abstract - Reefs in the Gulf of Aqaba are located at the northern boundary of the existence of photic tropical / subtropical reefs. This area was chosen to analyse the influence of specific abiotic and biotic factors on the carbonate deposition of stony corals. Compared to reefs, growing at low latitudinal conditions, minor growing rates were expected. Beside the decreasing growth rates along the bathymetric (light) - gradient, significant differences between the growth rates during the four seasons should be detectable.

The buoyant-weight technique (JOKIEL *et al.*, 1978) was used for measuring the net growth (carbonate deposition) of whole coral colonies.

Growth rates were measured for 14 coral species, growing in depths of 2-5, 10, 20 and 40m. The corals were weighted every three weeks over a period of two years. During the same time the water temperature, the light intensity and the amount of available POM (sediment and seston) was measured.

The results of the two years studies indicate a wide variability in the growth rates of different coral species. *Stylophora pistillata* shows the highest, *Mycedium elephantotus* and *Porites* sp. the lowest carbonate deposition. The growth rates of all species decreased with increasing depth.

The investigations showed no remarkable influence of heterotrophic nutrition or water temperature upon increment of mass. It seems that the light-intensity and the daily illumination-period were the main growth-limiting factors under the "suboptimal" conditions in the Gulf of Aqaba.

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NEW PALAEOECOLOGICAL DATA ON REEF FISH FAUNA FROM MONTE BOLCA (ITALY)

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Abstract - The Eocene fish fauna from Bolca constitutes one of the most important fossil fish assemblages in the world. Over 250 species and 140 genera have been classified. All the species are only fossil, but 10% of the genera are still living, while at the family level this percentage increases up to about 50%, and with the exception of the Pycnodontiformes, all the 19 orders are living.

The Bolca fish fauna has always been considered a reef fish community due to the presence of several reef fish families.

Studies on the spatial distribution of living reef fishes have made it possible to distinguish different populations within the reef whose composition and structure are closely related to the complexity of their habitats.

Furthermore, biomass and diversity increase when tidal lagoons, mangroves, sea-grass beds, etc. are present in the surrounding areas.

In the reef area three different fish populations can be recognized: those from the sand and/or prairie zone, the madrepore zone and the perireefal-pelagic zone.

In our opinion, the high percentage of living families or the close taxonomic relationship of the fossil fishes in the Bolca association with present-day fishes, makes it possible to apply actualistic data to them.

Three characteristic reef associations have been recognized. In particular, the sand and/or sea-grass bed population is quite differentiated and consists of 20 families (Bothidae, Fistularidae, Siganidae, Labridae, Mullidae, etc.); the reef population has 17 families, even though most of them are not "obligate reef" fishes (Serranidae, Acanthuridae, Tetraodontidae etc.); the reefal-pelagic population, which is more complex and numerically the largest of the three, consists of 25 families (Carcharinidae, Carangidae, Sphyraenidae, Scombridae, Clupeidae, etc.).

Studies made on the trophic and structural composition of this association, partly based on lists of fossil material collected since 1971, has allowed us to formulate more articulate palaeoecological hypotheses.

Lastly, the integration of palaeontological and sedimentological data has made it possible to reconstruct the principal features of the sedimentary complex and of certain characters of the Eocene environment at Bolca.

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LIGHTDEPENDENT ZONATION PATTERN OF XENIIDAE SPECIES IN THE RED SEA REFLECTING DIFFERENT MODES OF ADAPTATION TO LIGHT CONDITIONS (OCTOCORALLIA, ALCYONARIA)

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Abstract - Soft corals of the zooxanthellate family Xeniidae can occupy extended areas in Red Sea reef communities and prevent scleractinian corals from settlement and growth. From 1990 to 1992 studies were carried out on depth zonation and fluctuations of eight predominant species using the transect method of LOYA (1977) with transects of 10 m length at 10, 15, 20 and 30 m depth in selected areas of coastal fringing reefs at Aqaba (northern Red Sea) and at the Sanganeb-Atoll (central Red Sea).

A total of 15 species of Xeniidae was found to be present in the reefs near Aqaba 13 of which were found in the transects. The mean cover of Xeniidae ranged between 18 and 42 % of the transect dis-

tances with standard deviations of 5 to 51 % showing different degrees of fluctuations. These were found to be highest between 10 and 20 m depth at a reef slope exposed northward and decreased with depth and southerly exposition. Fluctuation in scleractinian abundance ranged 3-8 % with a maximum value of 17 % at 10 m depth near Aqaba. Fluctuations in abundance of Xeniidae partly follow the seasonal changes of light and water temperature. Decrease during wintertime is compensated for by next summers breed and rapid vegetative propagation.

Although species of the Xeniidae are known to be highly adaptable towards abiotic conditions the relative abundance of single species in the transects near Aqaba revealed a zonation of the preferred depth ranges down to about 40 m depth. The predominant species showed a sequence of successive replacement following the depth gradient (viz. *Xenia macrospiculata, X. umbellata, Heteroxenia ghardaqensis* (not always present), *X. obscuronata, X. faraunensis, X. benayahui, X. verseveldti, X. novaecaledoniae).* This pattern is supplemented by patches of less abundant species or single colonies (viz. *X. impulsatilla, X. biseriata, Anthelia glauca, Sympodium caeruleum* and *Heteroxenia fuscescens*).

A similar distribution was recorded at a reef slope of the Sanganeb-Atoll (orientation towards SSE, leeward slope) showing an absolute depth range of Xeniidae down to about 70 m. The sequence known from Aqaba was found to be expanded by four species moving in between 2 to 15 m depth: *X. grasshoffi, X. garciae, X. blumi* and *X. crassa. X. umbellata* is missing in the area, the rest of the sequence (see above) shifted downwards.The 1%- surface-irradiance level was found in Aqaba at 35-40 m, at Sanganeb at 70-80 m depth.

The zonation of species in areas showing high abundance of Xeniidae follows the depth gradient. Experimental translocation of five species to decreasing light levels (approx. 20-1% surface irradiance) showed different modes of adaptation. Under reduced light conditions the colony sizes of all species in the experiment increased mainly by extension of polyps. This provides larger surface area for the exposition of zooxanthellae. Further, after one year in the experiment for each species densities of zooxanthellae in the tissues and contents of photosynthetic pigments were determined and compared to control colonies, that had not been relocated. The results demonstrate 3 different modes of adaptation to the prevailing light conditions:

* *X macrospiculata* showed significant negative correlation of chlorophyll contents with the light gradient in the experiment. The symbionts seem to adapt to high light levels by reducing the number of photosynthetic units (PSU) in the cells (photoacclimatization). The species therefore can colonise the well illuminated shallow water zones in the reefs - we find it in the upper part of the zonation pattern.
* *X. faraunensis* and *X. obscuronata* showed no relation of density of zooxanthellae or chlorophyll contents to the prevailing light conditions. In X. faraunensis a significant negative correlation with the peridinin content of zooxanthellae and positive correlation of the clorophyll c2/a-ratio was found. Thus they increase the amount of antenna pigments in the PSU. Both species seem to have limited capacity to adapt to light conditions and thus are restricted to a certain range of moderate illumination - they dominate the central range of the depth distribution pattern.
* *X. benayahui* and *X. novaecaledoniae* showed significant negative correlation of densities of zooxanthellae in the tissues with the experimental light conditions. Under low light levels they increase the surface of colonies, the density of zooxanthellae and the amount of chlorophyll c_2 in the PSU. This adaptation permits them to colonise the deeper reef slopes with comparably low light intensities. They were found at the bottom end of the zonation pattern.

The light intensities available are regarded as the dominating factor governing the distribution of syn topic zooxanthellate Xeniidae species in areas with favourable conditions (low currents, little sedimentation).

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PALAEOECOLOGY OF PALAEOGENE CORALS FROM THE WESTERN DESERT, EGYPT

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Abstract - In the Palaeogene of the Western Desert of Egypt coral growth occurs in several stratigraphic levels and in different palaeoecological environments.

The middle to late Paleocene limestones of the Kurkur Formation of Abu Tartur Plateau (NW of Kharga Oasis) show small coral patch reefs with maximal lateral extension of about 150x300m. The most important framework builders are meandroid *Pachygyra* and massive growing *Astrocoenia* species. Other members of the coral fauna are *Leptoria*, *Siderastrea*, *Dimorphastrea* and *Montastrea*. Growth forms (mostly hemispherical, massive and branching) and sizes of the corals suggest a shallow neritic environment. During the Paleocene the present-day Abu Tartur Plateau was a palaeogeographic high on which a carbonate platform evolved. Therefore no or only little terrigenous influence disturbed coral growth.

Lower Eocene (early to middle Ilerdian) strata of the Farafra Oasis area show two levels with coral growth. In the shaly sediments of the Esna Formation, corals grew on a bioclastic layer. The coral fauna consists mainly of solitary (*Pattalophyllia, Placosmiliopsis, Trochosmilia)* and only one colonial form (*Stylocoenia*). The associated foraminiferal assemblage suggests a shallow marine environment. Coral growth was restricted to a very short timespan in which the input of fine terrigenous material was low.

The following limestones of the Farafra Formation were deposited in a shallow marine to lagoonal environment. Coral biostromes and gastropod layers are developed in the upper part. Facies association of lateral deposited sediments show a seagrass-meadow like environment indicating a high sedimentation rate of micritic carbonate. The coral biostromes are dominated by branching (*Goniopora elegans*) and cone-shaped forms (*Goniopora* n.sp.). Both forms are well adapted to high sedimentation rates. Elevated structures built by corals are not developed because of the lack of available accommodation space.

Although there may be evolutionary reasons for the low diversity of Palaeogene corals, the two examples from the Farafra area show that in this case the low diversity is due to the environmental conditions (high sediment input) detrimental to coral growth.

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FACIES-CONTROLLED DISTRIBUTION OF RUDIST-BIVALVES IN THE LATE CRETACEOUS OF BEOTIA, CENTRAL GREECE

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Abstract - Rudist-bivalves are widely distributed in transgressive calcareous deposits along the Pelagonian continental fragment which is exposed in Beotia, Central Greece. During the Late Santonian-Campanian, rudist communities were dominated by *Vaccinites cornuvaccinum* (Bronn) which is preserved in life position at several localities. Rather diverse radiolitids and a single caprinid

species are associated. Former depositional environments have been reconstructed by microfacies analyses of several sections.

Rudist-bivalves were found to occur frequently as soon as the associated biofacies and stable isotope composition of embedding carbonates indicate normal marine conditions of subtidal sedimentation. Within their biostromes and pseudocolonies biotic diversity is poor, only miliolid foraminifera, few encrusting Ostreidae, and indications of bioeroding sponges are frequently found. In contrast to other fossil and extant tropical shallow-water communities, the biotic diversity of the analysed rudist biostromes, therefore, appears to be remarkably impoverished. Only the seaward debris fans of high-energy *Gorjanovicia* and *V. cornuvaccinum* shoals are characterized by abundant and diverse foraminifera and a variety of binding and encrusting Squamariaceae, problematic algae and Cyanophyceae.

Because of the development of several growth morphotypes, *V. cornuvaccinum* was adapted to environments of different water agitation and sedimentation rates. These habitats comprised lagoonal soft bottoms with minor sediment supply as well as shoals and their landward slopes. In turbulent environments pseudocolonies of numerous erect shells developed and acted as sediment bafflers. Geniculate and curved morphotypes indicate repeated toppling and change in growth direction as the growing shells were not stabilised by slowly accumulating sediment in lagoonal environments.

Most radiolitids proved to be more stenotopic. Their morphology and growth habits can be related to prevailing sedimentary conditions. Elongate, compact-shelled species of *Gorjanovicia* preferred more turbulent environments, where they formed dense communities. Few individuals lived on the seaward slopes of these banks. Because of thick, massive shells and high vertical growth rates they were able to cope with sporadically high supply of bioclastic debris. The recumbent *Mitrocaprina boeotica* (Munier- Chalmas) thrived in lagoons with slow sedimentation.

Growth rates of several shells of *V. cornuvaccinum* have been determined by stable isotope sclerochronology and give additional information about the adaptation of different morphotypes to vari ous depositional environments.

SCLEROCHRONOLOGY

HIGH RESOLUTION ANALYSIS AND ANNUAL VARIATION OF TRACE ELEMENTS IN SPECIES OF THE CORAL *Porites* FROM MAURITIUS ISLAND (INDIAN OCEAN)

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Abstract - The anions phosphate, sulphate and nitrate, and the heavy metals Cd, Co, Cu, Fe, Mn, Ni, and Zn incorporated in the aragonitic skeletons of corals (*Porites solida* and *P. lutea*) were analysed using Ion Chromatography. Trace element contents of thirty coral samples from different parts of the reef complex of Mauritius Island were compared.

The concentrations in the samples differ with location. Heavy sediment load and increased input of nutrients and heavy metals to the fringing reef can be correlated with increased incorporation of trace elements in *Porites* colonies. Corals with high nutrient concentrations reflect the high eutrophication level of the sampling sites. Increased input of heavy metals into parts of the reef complex can be correlated with high trace metal concentrations in the *Porites* skeletons of the same sampling sites. High amounts of heavy metals together with increased nutrient contents in coral skeletons may be responsible for inhibition of coral growth.

The sclerochronological record of trace element variation in Recent *Porites* colonies was investigated. Annual changes in chemical composition of the carbonate skeletons were compared to variations in rainfall, seawater-temperature, strong cyclones and years with worldwide coral-bleaching events. There are no significant secular variations of incorporation of anions into the *Porites* skeletons. In different colonies maximum and minimum concentrations occur in different years. Time scale analyses of nitrate, phosphate and sulphate in the *Porites* samples from the same reef complex cannot be correlated.

There is no positive correlation between longterm variation in rainfall or changes in seawater-temperature and anion concentrations in corals. Trace element incorporation into the *Porites* skeletons shows no evidence for "event"-years in the Mauritius reef complex.

Only the annual variations of Nickel show similar trends in corals from the same sampling site. Nickel-concentrations in yearly density bands can be correlated with annual rainfall-data of Mauritius Island. The application of "similarity-coefficients G(x,y)" shows positive correlations. Nickel is a good indicator for evaluating yearly varying Ni-input into the reef complex. Years with strong cyclones and strong rainfall can be recognized in the Ni record of *Porites* colonies.

1. INTRODUCTION

Man-made pollution is an increasing problem in tropical marine environments. Heavy sediment loads may be lethal to corals and lesser quantities may inhibit coral growth, cause changes in growth forms or alter the species composition of reef-building communities (PASTOROK & BILYARD 1985). The littoral ecosystem of Mauritius Island (fringing reef) is degenerating because of coral diseases, widespread eutrophication and algal growth in some parts of the reef and degradation of lagoons. An increase of sea urchins population, reduction in coral vitality and decrease of coral diversity can be observed (HOTTINGER *et al.* 1990). A geochemical study was undertaken using the widespread Recent coral genus *Porites* to investigate possible reasons for reef degradation (IMMENHAUSER-POTTHAST 1994).

Anthropogenic inputs of sewage could be responsible for the degradation of the corals in the Mauritius reef system because of nutrients or toxic heavy metals (MULLER *et al.* 1991). There are several sources of pollution that could affect the coastal environment of Mauritius Island, e. g. a sugar cane industry, waste dump sites, and domestic sewage. In addition, there is an industrial region in Port Louis harbour. Nutrients, pesticides and heavy metals are washed out by strong rainfall during the rainy season and are transported into the lagoon by rivers, canals and groundwater.

In this study the incorporation of potentionally detrimental substances such as nutrients and heavy metals into the coral skeleton was examined to evaluate the possible role of these trace elements in affecting the reef ecosystem. Annual changes in chemical composition of the carbonate skeletons (aragonite) were compared to variation of rainfall, seawater-temperature, strong cyclones and years with worldwide coral-bleaching events, to see if changes of climatological and ecological parameters influence the composition of coral skeletons. Ion Chromatography (IC) was used to determine both anions (nitrate, phosphate, sulphate) and heavy metals (Cd, Co, Cu, Fe, Mn, Ni, Zn) in the aragonitic skeletons of reef-building corals.

2. MATERIAL AND METHODS

2.1. Sample preparation

Thirty coral samples from different parts of the reef complex (0.4 - 18.0 m water depth) were analyzed using Chelation Ion Chromatography. Samples were taken from eutrophicated lagoons (Trou d'Eau Douce, Tamarin), estuaries (Grande and Petite Rivière Noire) and polluted reef sites (Port Louis), as well as from unaffected areas (Flic en Flac; Ile Plate), to determine background concentrations (see Fig. 1).

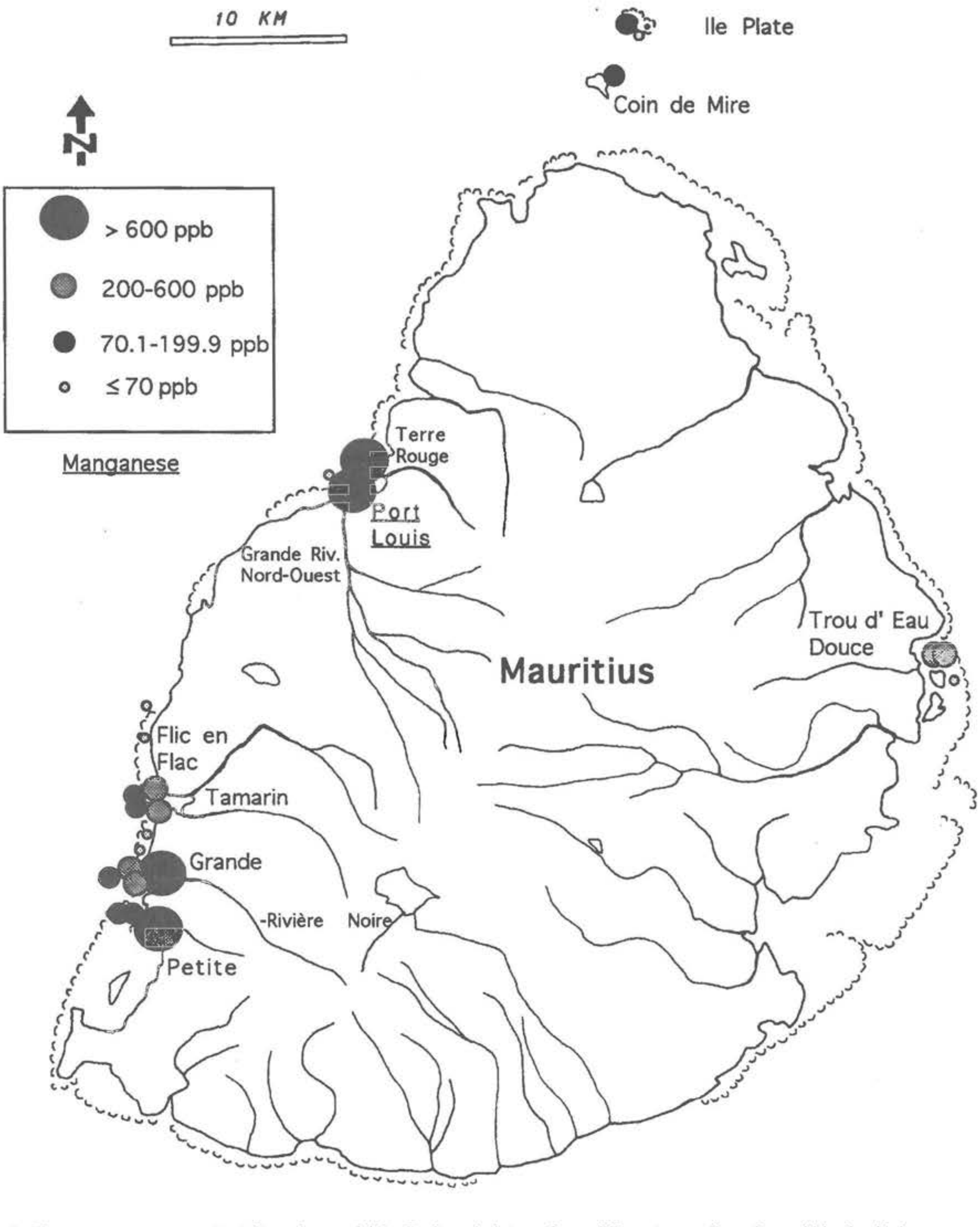


Fig. 1. Mean manganese content (in ppb = ng/g) in *Porites* skeletons from different sampling sites within the Holocene reef complex of Mauritius Island. Each circle represents a coral sample. Increasing Mn-concentrations are indicated by increasing diameters of the circles. Highest manganese content occured in corals from sampling sites near estuaries and freshwater inflow. Manganese content in coral skeletons decreases with increasing distance from the coastline.

Massive, hermatypic colonies of the Recent scleractinian species *Porites solida* and *Porites lutea* were used. *Porites* were chosen because of their widespread occurrence and because their growth record can be dated by density bands in the skeletons. Six massive coralla (representing 10-40 years of growth) were sawed into 5 mm slabs and x-rayed. In the x-ray positive a pair of high- and low-density bands shows the annual growth rate of the coral colony. Using these density bands each coral was dated from the date of sampling to the beginning of colony growth. For the sclerochronological investigation annual samples of each colony were prepared and analyzed. Aquatic solutions of bleached, cleaned, oven-dried coral powders of each coral sample were injected into the Ion Chromatography-System. All cleaning and preparation proceedings and more detailed information about the method, calibration, blank concentrations, and verification of analyses are given elsewhere (SHOTYK & IMMENHAUSER-POTTHAST 1995; DIONEX 1992).

2.2. Chelation Ion Chromatography

Anion analyses were done by Ion Chromatography with an analytical column AS4A using a 250 µl injection loop. For the measurement of transition metals Chelation Ion Chromatography (CIC) was performed using a Dionex 4500i IC System with two separator columns: 30 g of sample was concentrated on-line by pumping the solution through the MetPac CC-1 chelating concentrator column at a rate of 3 ml per minute. The MetPac is then rinsed with high purity 2 M ammonium acetate to remove alkaline earth metals. The transition metals are then eluted to a second concentrator column (TMC-1) using 2 M *Suprapur* HNO_3. The TMC-1 is then converted to a salt form using 0.1 M NH_4NO_3, and then switched on-line with the analytical column, the IonPac CS-5. We used two IonPac CS-5 columns in series. Using only one column, separation of Zn and Co is incomplete and determination of Cd is impossible, because it will be masked by Zn and Co. The concentrated metals are then eluted using 6 mM PDCA (pyridine-2,6-dicarboxylic acid) / 0.4 M NaOH; the pH of this eluent is 4.4. After the separated metals leave the column they are complexed by 0.5 mM PAR (4-[2-pyridylazo] resorcinol), a metallochromic indicator. Absorbance is measured in a Dionex UV-Vis detector at 520 nm.

With these methods the detection limits in the sample solutions are as follows: 23 ppb (ng/g) NO_3^-, 18 ppb PO_4^{3-}, 34 ppb SO_4^{2-}, 5 ppb Fe, 2 ppb Zn, 0.3 ppb Cd, 0.2 ppb Cu, 0.1 ppb Co, 0.1 ppb Ni, and 0.1 ppb Mn.

3. RESULTS AND DISCUSSION

The anions NO_3^-, PO_4^{3-} and SO_4^{2-}, and the heavy metals Fe^{3+}, Cu^{2+}, Ni^{2+}, Zn^{2+}, Co^{2+}, Cd^{2+} and Mn^{2+} can be determined in the aragonitic skeletons of the coral genus *Porites* in trace to ultratrace concentrations. The average measured concentrations of these trace ions in thirty samples (± one standard deviation) are: NO_3, 30 ± 4.7 µg/g; PO_4, 63 ± 7.7 µg/g; SO_4, 630 ± 29.0 µg/g; Fe, 3 ± 0.3 µg/g; Cu, 680 ± 52 ng/g; Ni, 123 ± 23 ng/g; Zn, 790 ± 193 ng/g; Co, 85 ± 18 ng/g; Mn, 260 ± 41 ng/g (dry weight). Cd could be determined in only four coral analyses. The mean Cd-concentration in these samples is 40 ± 7 ng/g. Other measurements were below the detection limit (30 ng/g). These results represent similar concentration ranges as earlier published data for Ni, Cu, Fe, and Zn content in *Porites* corals (HOWARD & BROWN 1984; SWART 1979) and Mn-concentrations in *Pavona clavus* (LINN *et al.* 1990; SHEN *et al.* 1992).

The trace elements content of ten representative coral samples from the Mauritius reef complex are given in Tab. 1.

sample	**location**	**NO3** (ppm)	**PO4** (ppm)	**SO4** (ppm)	**Fe** (ppm)	**Cu** (ppb)	**Ni** (ppb)	**Zn** (ppb)	**Co** (ppb)	**Cd** (ppb)	**Mn** (ppb)
9184	Trou d'Eau Douce lagoon, submarine well	81.7	<0.2	499.1	2.2	150	10	2165	20	n.d.	480
9142	Coin de Mire slope	17.3	n.d.	615.9	4.9	90	<10	155	<10	n.d.	70
9182	Port Louis bay, harbour	50.0	438.1	686.8	3.5	520	580	22240	110	<30	820
9107	Flic en Flac reef flat	n.d.	86.3	642.5	0.4	215	10	<10	55	n.d.	<10
9108	Tamarin Bay northern coast	118.2	134.2	686.1	7.1	570	170	230	70	n.d.	610
9117	Tamarin Bay southern coast	72.4	76.1	727.5	10.4	560	610	8180	180	n.d.	540
9192	Grande Riv. Noire bay	43.0	201.4	636.2	18.1	330	290	3050	70	n.d.	440
9147	Grande Riv. Noire bay	32.0	168.9	616.8	9.6	160	140	2050	90	n.d.	240
9127	Petite Riv. Noire near estuary	0.8	n.d.	592.6	19.4	2420	820	3820	440	110	1890
9135	Petite Riv. Noire outer lagoon	13.2	6.8	584.5	0.9	23	112	193	28	n.d.	82
mean concentr. of 30 Porites		**30.0**	**63.0**	**630.0**	**2.9**	**680**	**123**	**790**	**85**	**<30**	**260**
±one standard deviation		4.7	7.7	29.0	0.3	52	21	193	18	7	41

Tab. 1. Results of Ion Chromatography analyses (in ppb = ng/g, ppm = µg/g). Trace element concentrations in coral skeletons of *Porites* samples from different sampling sites within the Holocene reef complex of Mauritius Island (in dry weight). The standard deviation for each element is: NO3, 15.7%; PO4, 12.3%; SO4, 4.6%; Fe, 9.3%; Cu, 7.6%; Ni, 17.0%; Zn, 24.0%, Co, 14.0%; Cd, 16.3%; Mn, 14.9%. Sampling sites are indicated in Fig. 1.

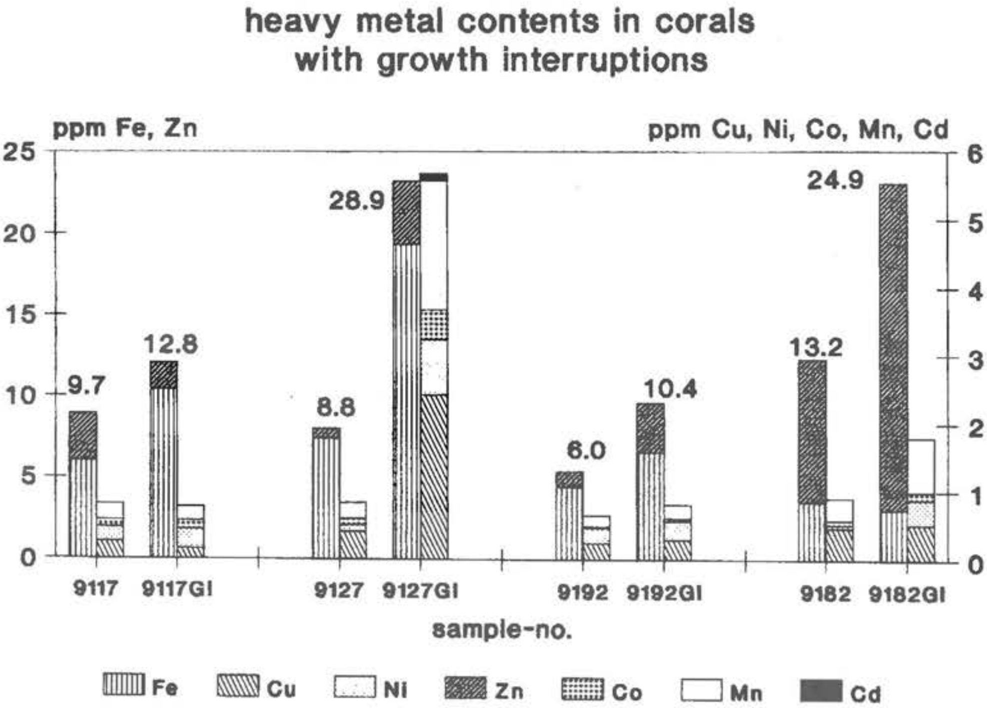
The concentrations in the samples differ with location: corals from turbid estuaries (like Grande Rivière Noire or Petite Rivière Noire) or from locations with input of sewage (Port Louis) show much higher concentrations than samples from unaffected areas (e. g. Flic en Flac and Coin de Mire) in the fringing reef (Tab. 1). Heavy metals are good indicators for the input of terrestrial matter. Manganese content of the coral skeletons can be perfectly correlated with inflow of freshwater into the lagoon. Corals from sampling sites near the coastline of bays and estuaries or with submarine groundwater inflow show much higher Mn-concentrations than samples from the fore-reef or from sampling sites far from the coast (Fig. 1, Tab. 1). Sulphate is the only trace ion with a relative constant concentration range in all samples.

Highest nutrient concentrations (max. 438 µg/g phosphate and >60 µg/g nitrate) were found in corals from sites with high eutrophication levels and from the lagoon in Trou d'Eau Douce with a submarine groundwater inflow.

Heavy sediment load and increased input of nutrients and heavy metals to the fringing reef can be correlated with increased incorporation of trace elements in *Porites* colonies in the Mauritius littoral ecosystem.

High heavy metal concentrations, especially the highest amount of Cd, could be determined in a coral sample from a turbid estuary (no. 9127, Petite Rivière Noire) with heavy sediment load. The maximum metal concentrations in this sample are (in ng/g dry weight): Fe, 19360; Cu, 2420; Ni, 820; Zn, 3820; Co, 440; Cd, 110; Mn, 1890. The coral colony shows interruptions of calcification, with stoppage of coral growth, sediment crusts and algal cover in the center of the colony.

Coral skeletons with growth interruptions often show high phosphate contents compared to samples with regular growth rates and unaffected colony growth. These samples also show higher heavy metal concentrations in parts of the skeletons with growth interruptions compared to healthy parts of the same corallum (Fig. 2). Duplicate analyses of four *Porites*-colonies with growth interruptions were done. Annual density bands of the skeletons with growth interruptions (samples "GI" in Fig. 2) show metal concentrations in an order of 130-320% higher than parts of the same corallum with normal growth (Fig. 2).



numbers at bars indicate the total metal concentration of a sample

Fig. 2. Heavy metal contents (in ppm = µg/g) in coral skeletons with growth interruptions. Duplicate analyses of four *Porites* colonies show higher trace metal concentrations in parts of the skeletons with growth interruptions. Annual density bands of the skeletons with growth interruptions (samples no. "GI") show metal concentrations in an order of 130-320% higher than parts of the same corallum with normal growth.

There are no significant secular variations of incorporation of anions into the *Porites* skeletons. Time scale analyses of nitrate, phosphate and sulphate in the *Porites* samples from the same reef complex cannot be correlated. In different colonies maximum and minimum concentrations occur in different years (Fig. 3, 4). Different corals show different trends of incorporation of the trace ions. In some cases nitrate and phosphate remain nearly constant during the whole growth period of the coral (sample no. 9147, Fig. 3). The sulphate record varies, but the sulphate peaks cannot be correlated to any climatological parameter of the Mauritius ecosystem.

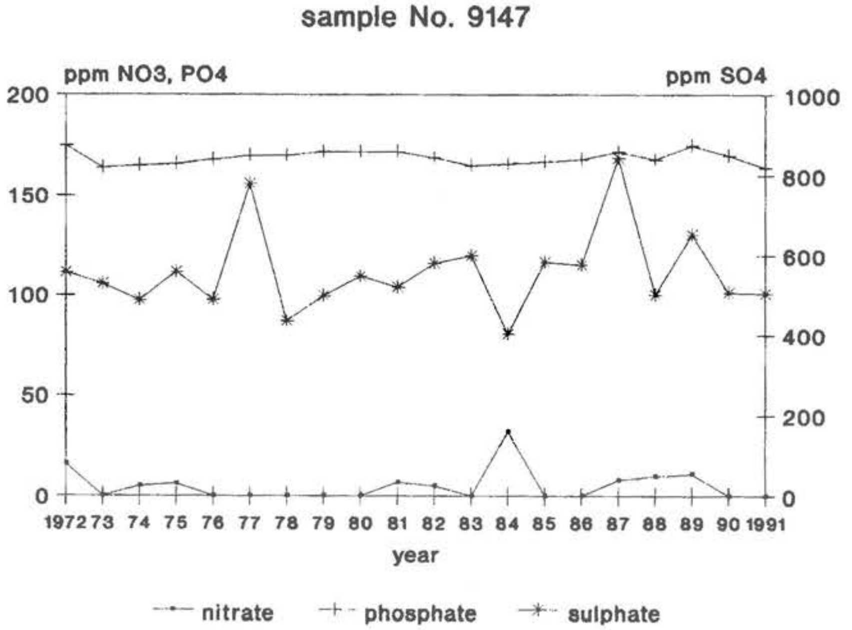


Fig. 3. Temporal variations of nitrate, phosphate, and sulphate concentrations in coral sample no. 9147 from Grande Rivière Noire Bay (Mauritius Island). Nitrate and phosphate concentrations remain nearly constant within the growth period of the coral colony.

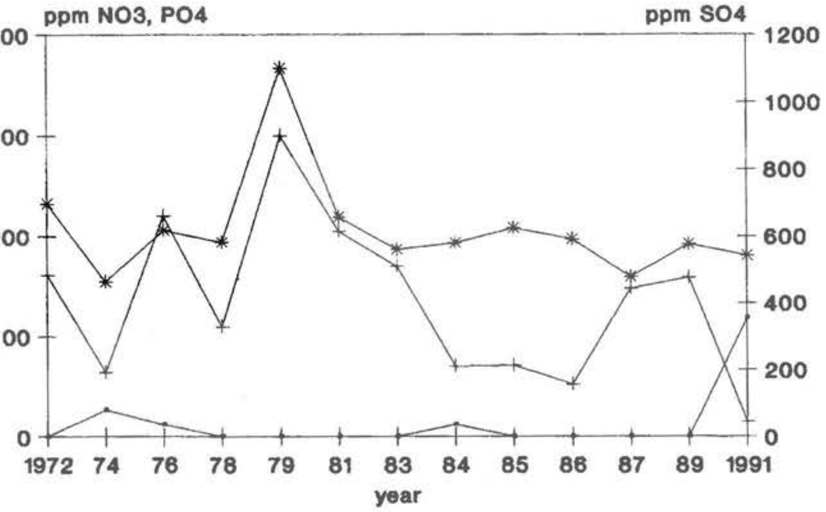


Fig. 4. Temporal variations of nitrate, phosphate, and sulphate concentrations in coral sample no. 9108 from Tamarin Bay (Mauritius Island). Peaks of phosphate and sulphate concentrations occur in 1979. Strong cyclones in Mauritius occurred in 1980 and 1983, coral-bleaching is known from 1983 and 1987. These "event"-years cannot be correlated with anion concentrations in the coral skeleton. A comparison with coral no. 9147 shows no comparable trend of trace ion incorporation into the skeletons.

Another example of a time scale analyses of anions shows a different trend (sample no. 9108, Fig. 4). Nitrate concentration is often under the detection limit, but has increased significantly since 1989. The phosphate content shows a clear variation in time, but minimum and maximum concentrations of phosphate occur in different years compared to the other investigated corals. Peaks of phosphate and sulphate concentrations in this skeleton occur in 1979 (Fig. 4). Strong cyclones in Mauritius could be registrated in 1980 and 1983, coral-bleaching is known from 1983 and 1987 (PADYA 1984; GLYNN 1983; GEISTER 1992). These "event"-years cannot be correlated with anion concentrations in the coral skeletons.

There is no correlation between annual variation of rainfall or changes in seawater-temperature and anion concentrations in corals. Trace element incorporation into the *Porites* skeletons shows no evidence for "event"-years in the Mauritius reef complex. Years with strong cyclones and therefore with strong rainfall and increased input of terrestrial matter cannot be recognized in the trace ion record of the samples.

In addition, there are no significant secular trends in the time scale curves of the heavy metals Co, Fe, Mn, and Zn incorporated in the density bands of the *Porites* colonies. Only the annual variations of Ni - and in one case of Cu - show the same trends in corals from the same sampling site (Fig. 5). The curves of the Ni record of two corals of Grande Rivière Noire Bay (SW reef complex) show similar trends in time. Elevated Ni contents could be determined in both coral skeletons in the same time period (Fig. 5).

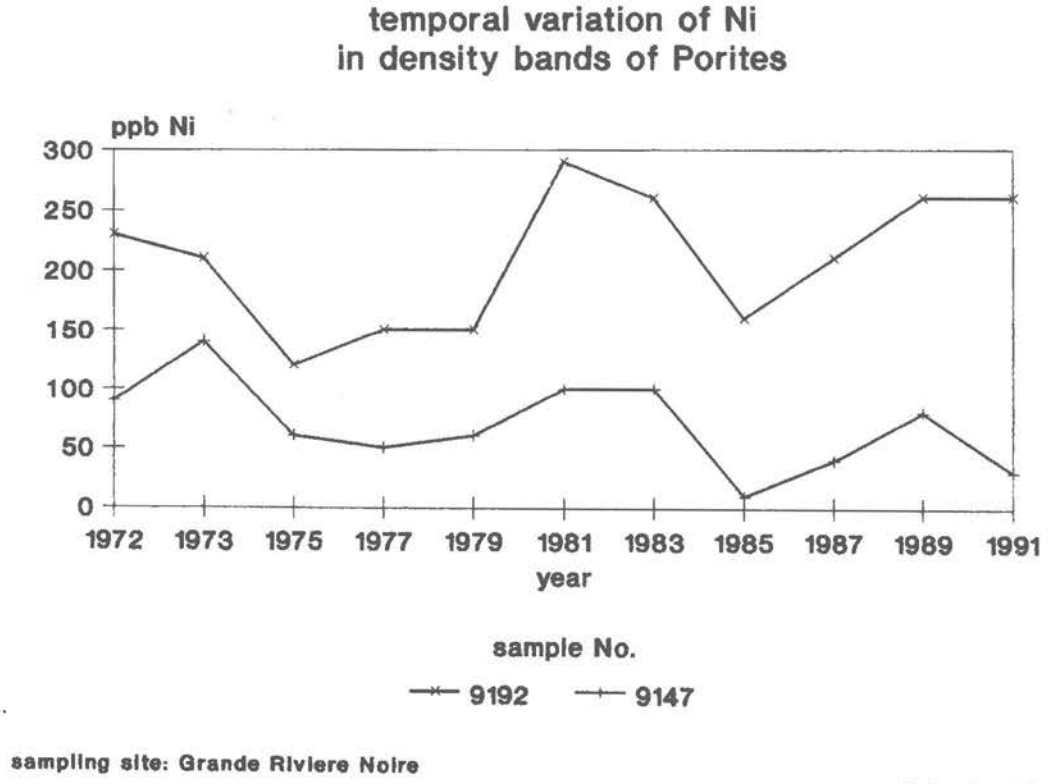


Fig. 5. Annual variation of Ni-concentrations in two coral samples from Grande Rivière Noire Bay in SW-Mauritius. The curves of the Ni record show similar trends in time. Elevated Ni contents could be determined in both coral skeletons in the same time period.

The elevated Ni concentrations refer to decreased input of Ni into the ecosystem. Residually enriched Ni of the tropical soils of the volcanic island can be washed out by strong rainfall and is transported into the reef system (OGUNSUA *et al.* 1993). Nickel-concentrations in yearly density bands of coral samples can be correlated with annual rainfall data from Mauritius Island (Fig. 6). High amounts of rainfall and high concentrations of Ni in the coral skeleton occur in the same years. The application of the so called "similarity-coefficient" G(x,y) of two curves (according to SCHWEINGRUBER 1983) shows a good correlation (Fig. 6). G(x,y) is 86 % in this case, 100 % would be perfect, better than 50 % is acceptable.

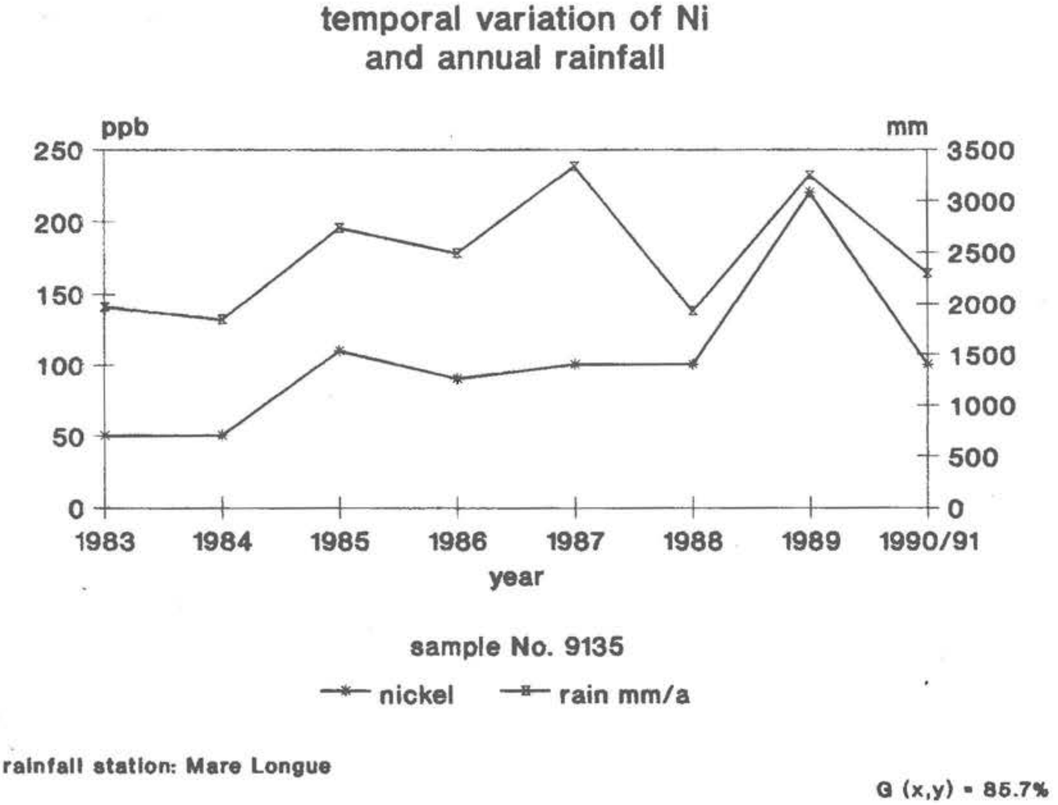


Fig. 6. Correlation of annual Ni-concentrations in coral sample no. 9135 from Lagoon of Bénitiers, offshore the Petite Rivière Noire Bay, with annual rainfall in SW-Mauritius. The correlation coefficient G(x,y) = 85.7 % indicates a positive correlation.

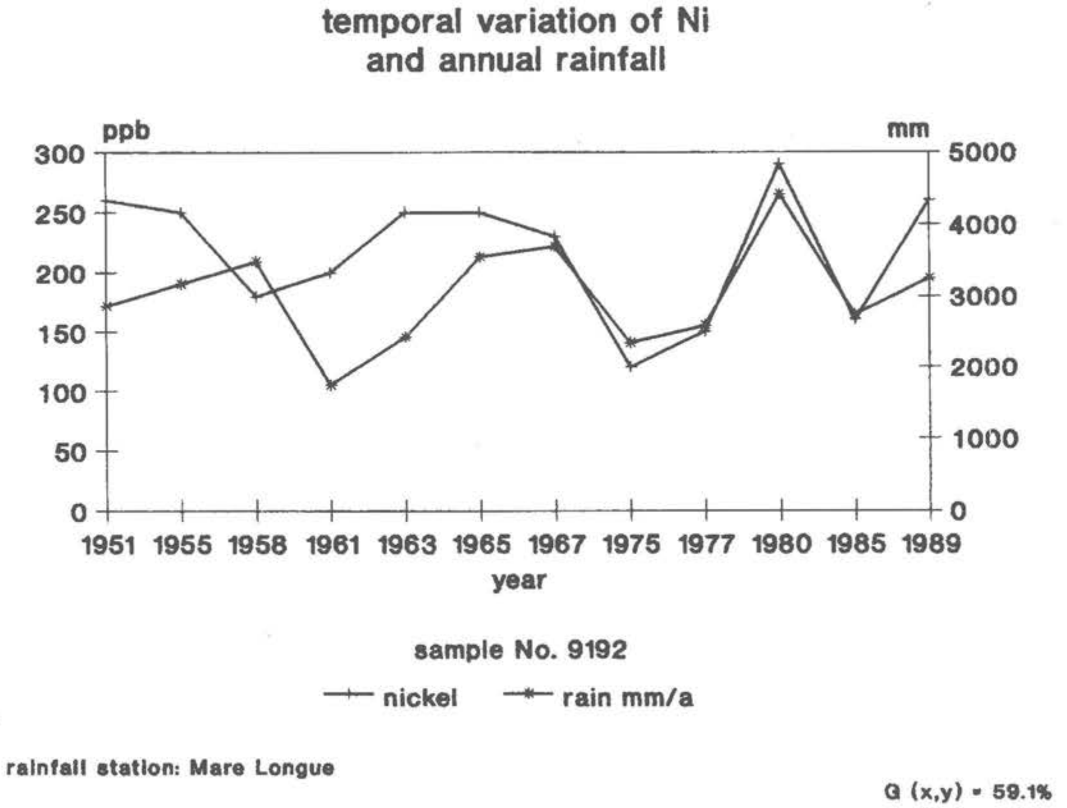


Fig. 7. Correlation of annual Ni-concentrations in coral sample no. 9192 from Black River Bay with annual rainfall in SW-Mauritius. Increased metal concentrations in the skeleton are related to an increased amount of rainfall in the same time period. Decreasing amount of rainfall and temporal Ni-contents of the colony show the same trend.

Another example for this positive correlation can be seen in sample no. 9192, the oldest investigated coral (Fig. 7). Increased metal concentrations in the skeleton are related to an increased amount of rainfall in the same period. Decreasing amount of rainfall and temporal Ni-contents of the *Porites* colony show the same trend. Only in older parts of the colony this similar trend is not as clear as in the last thirty years of growth. Alteration, e. g. early diagenesis, of the oldest parts of the coral may have affected the primary chemical composition of the skeleton (POTTHAST 1992). In this case the similarity coefficient G(x,y) is ±60 % (Fig. 7).

4. CONCLUSIONS

The heavy metals Cd, Co, Cu, Fe, Mn, Ni, and Zn and the nutrients phosphate and nitrate are useful indicators to investigate ecological problems of the Mauritius littoral ecosystem. The sulphate analyses of the *Porites* samples don't give any satisfying results referring to this problem.

Heavy sediment load and increased input of nutrients and heavy metals to the fringing reef can be correlated with increased incorporation of trace elements in *Porites* colonies in the Mauritius littoral ecosystem. Corals with high nutrient concentrations reflect the high eutrophication level of the sampling sites. Increased input of heavy metals into parts of the reef complex can be correlated with high trace metal concentrations in the *Porites* skeletons of the same sampling sites.

High amounts of heavy metals together with increased nutrient contents in coral skeletons may be responsible for inhibition of coral growth.

There are no significant variations in time of incorporation of anions and of most heavy metals into the density bands of *Porites* skeletons.

The sclerochronological variations of trace ions in coral skeletons are not very useful to show climatical respectively environmental changes in the Mauritius reef ecosystem.

Only Nickel is a good indicator to evaluate yearly varying Ni-input into the reef complex. Ni in density bands of coral skeletons can be correlated with annual rainfall data. Years with strong cyclones and strong rainfall and therefore with increased input of terrestrial matter into the reef complex can be recognized in the Ni record of *Porites* colonies.

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LONGTERM ISOTOPIC TRENDS FROM CARIBBEAN DEMOSPONGES: EVIDENCE FOR ISOTOPIC DISEQUILIBRIUM BETWEEN SURFACE WATERS AND ATMOSPHERE

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Abstract -Three specimens of the demosponge *Ceratoporella nicholsoni* sampled off Jamaica in different water depths were investigated for their stable isotope compositions. *Ceratoporella nicholsoni* precipitates aragonite in isotopic equilibrium with ambient sea-water. Oxygen isotope signals are in equilibrium with measured temperatures and salinities with no significant variations in $\delta^{18}O$ from 1800 to 1990. Carbon isotopes reveal a distinct decrease from +4.8‰ in 1800 to +4.0‰ in 1990. Whereas the carbon isotopic composition of atmospheric CO_2 decreased by -1.4‰ during the same time period, sponge aragonite records only a -0.8‰ decrease. A pre-industrial isotopic disequilibrium between Caribbean surface water CO_2 and atmospheric CO_2 as well as an increasing disequilibrium mostly during the last 30 years become obvious after calculating $\delta^{13}C$ of CO_2 in isotopic equilibrium with sponge aragonite. This study shows that demosponges serve as long-time recorders of isotopic changes in surfaces waters and can provide valuable data to calculate the oceanic uptake of CO_2.

1. INTRODUCTION

The demosponge *Ceratoporella nicholsoni* (Hickson 1911) lacks zooxanthellate algae and precipitates aragonite extracellularily in isotopic equilibrium with ambient sea-water (REITNER 1992). DRUFFEL & BENAVIDES (1986) were the first to make use of this property in an attempt to calculate the uptake of anthropogenic CO_2 by the ocean. Investigations by WILLENZ & HARTMAN (1985) and BENAVIDES & DRUFFEL (1986) revealed average growth rates of *C. nicholsoni* ranging from 100 to 250 µm/year. The sponge tissue inhabits small calicles on the surface of the basal skeleton, which are filled after some years with additional aragonite. Thus, records of seasonal or annual changes of the isotopic composition are not accessible with current sampling methods, but skeletal aragonite of demosponges can serve as an accurate recorder of shallow-water $\delta^{18}O$ and $\delta^{13}C_{DIC}$ on time scales measuring in decades or centuries.

We attribute *Ceratoporella nicholsoni* (Hickson 1911) to the class Demospongiae following VAN SOEST (1984), VACELET (1985) and REITNER (1992) who doubted the monophyly and justification of a separate class "Sclerospongiae", erected by HARTMAN & GOREAU (1972). As stated by these authors, the calcareous basal skeleton, weighted very high by HARTMAN & GOREAU (1972), is an archaic feature of the Demospongiae. The so-called "Sclerosponges" (sponges with siliceous spicules and basal skeleton) have to be attributed to different taxa within the Demospongiae according to their spiculation.

2. MATERIAL AND METHODS

One of the authors (H. L.) collected several specimens of *Ceratoporella nicholsoni* off northern Jamaica from the deep fore-reef off Discovery Bay (water depth 80-90 m) and in a reef tunnel at 25 m depth at Rio Bueno. Three specimens were investigated for their oxygen and carbon isotopic compositions with a Finnigan Mat 252 mass spectrometer at the Geological Institute, University of Erlangen. Isotopic ratios are reported in permil relative to the PDB standard. External precision (2σ) of the analyses is ±0.06‰ for $\delta^{18}O$ and ±0.05‰ for $\delta^{13}C$. Temperatures were calculated using the equation given by O´NEIL *et al.* (1969) and an aragonite correction of -0.7‰ (WEFER & BERGER 1991).

3. DATING AND GROWTH RATES

Due to the lack of visible growth bands we assumed constant growth rates to calculate the age of a part of the skeleton. The growth rate of one specimen (Rio Bueno, 25 m) was calibrated by ^{14}C AMS-analysis against bomb radiocarbon curves for the Caribbean and Florida Straits (DRUFFEL 1989; BENAVIDES & DRUFFEL 1986). Eight samples closely embracing the expected position of the bomb-test induced ^{14}C enriched skeletal parts were investigated. Growth rates of the other specimens were determined by linear regressions between $\delta^{13}C$ values of the unknown specimen and corresponding $\delta^{13}C$ values of the dated Rio Bueno specimen at the same distance from the outer rim. The age of the outer rim of all specimens corresponds to the date of sampling. The $\delta^{13}C$ values of these youngest skeletal parts are identical. Thus, the slope of the resulting regression line multiplied with the growth rate of the ^{14}C dated specimen gives the unknown growth rate.

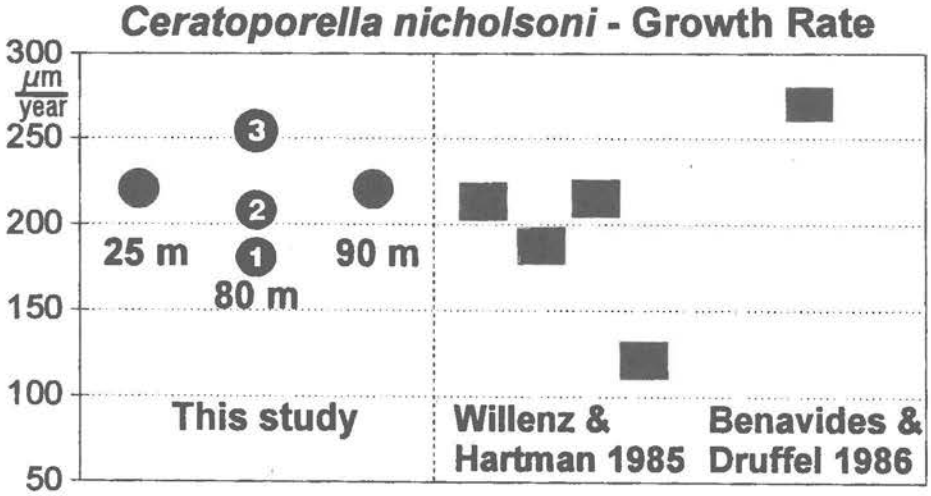

Fig. 1. Growth rates of three specimens of *C. nicholsoni* from Jamaica: Rio Bueno, 25 m, Discovery Bay, 80 and 90 m. For one specimen we calculated three different growth rates labeled 1 (old) through 3 (young). Growth rates agree with determinations of WILLENZ & HARTMAN (*in situ* staining technique, 28 m depth, Jamaica). BENAVIDES & DRUFFEL found slightly higher rates ($\Delta^{14}C$ and ^{210}Pb chronologies, 26 m depth, Jamaica).

We observed a growth rate (Fig. 1) of 220 µm/year for the 25 m specimen and the 90 m specimen (Pearson correlation coefficient r=0.99, n=15). A specimen from 80 m shows varying growth rates on the order of 180 µm/year in the oldest part (before 1880, r=0.79, n=7), 210 µm/year (1880 to 1960, r=0.94, n=24) and 260 µm/year in the youngest part (1960 to 1990, r=0.98, n=8).

To use this method of dating, we have to assume that the carbon isotopic composition was identical in shallow and deep water during most of the lifetime of the sponges. This assumption is plausible as all specimens grew above the thermocline, in the well mixed surface layer. It is further supported by the identical $\delta^{13}C$ values of the youngest growth layers, which are known to be of the same age. Moreover, the heaviest values in shallow and deep water, assumed to represent the "pre-industrial plateau" (steady state of the atmosphere before approx. 1830, Fig. 4), are nearly identical. Of course, this method prevents any further conclusions drawn from comparisons of deep and shallow water $\delta^{13}C$.

4. OXYGEN ISOTOPES AND WATER TEMPERATURES

Neither the shallow nor the deep water specimens reveal a characteristic $\delta^{18}O$ trend during the recorded time interval from about 1800 to 1990. Most values scatter around -0.5‰ (80-90 m) or -0.7‰ (25 m). At measured salinities of 36.1‰ at Chalet Caribe Reef, Montego Bay (DRUFFEL & BENAVIDES 1986) and 36.9‰ in the more restricted Discovery Bay (PIGOTT & LAND 1986) and a corresponding $\delta^{18}O_{water}$ of +0.8‰ (SMOW, LAND 1992), the oxygen isotopic data reflect mean water temperatures of 25°C (80-90 m) and 26°C (25 m). These values are in good agreement with temperatures measured during sampling. The calculated temperatures range from 24.5°C to 25.3°C in deeper water and from 25.4°C to 26.3°C in shallow water (Fig. 2). FOLLAND *et al.* (1990) reported a sea-surface temperature rise of 0.7°C for the subtropical North Atlantic during the 20th century. Considering the analytical precision of ±0.06‰ for $\delta^{18}O$ that corresponds to ±0.3°C, the observed temperature rise is too small to be reliably recorded by the $\delta^{18}O$ values of *C. nicholsoni.*

5. CARBON ISOTOPES

The longterm $\delta^{13}C$ trends (Fig. 3) of two of our specimens (25 m and 90 m) display only minor scatter compared to our third specimen (80 m) and to previously published data (NOZAKI *et al.* 1978, DRUFFEL & BENAVIDES 1986). All investigated individuals show a decrease in $\delta^{13}C$ from +4.8‰ in the oldest parts (about 1800) to +4.0‰ in the youngest parts (1990) of the skeletons (Fig. 4). From 1800 to 1960

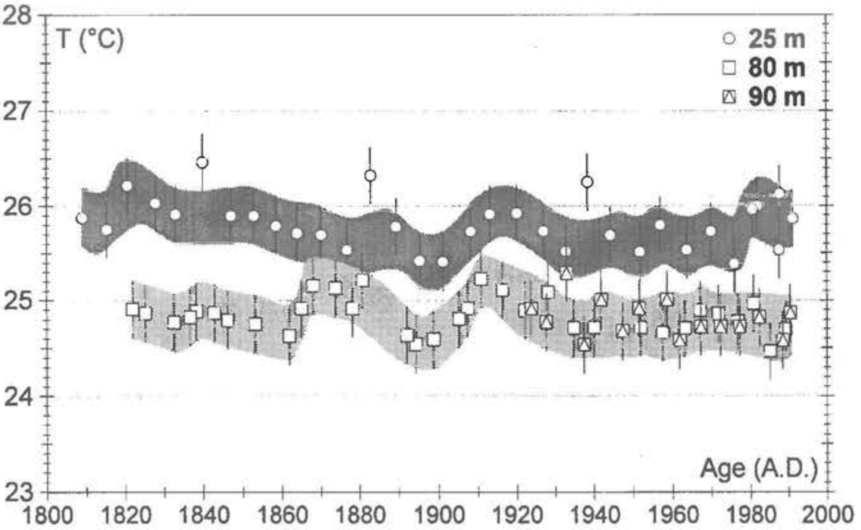

Fig. 2. Water temperatures north of Jamaica calculated from $\delta^{18}O$ of *C. nicholsoni* at 25 m (Rio Bueno) and 80-90 m depth (Discovery Bay). Error bars correspond to ±2 σ of $\delta^{18}O$. Age designations before 1890 for the 80 m specimen are uncertain.

$\delta^{13}C$ values gradually decreased from +4.8‰ to 4.45‰. During the last 30 years $\delta^{13}C$ values drastically decreased by another -0.45‰. These trends are in very good agreement with the observed increase in atmospheric pCO_2 (Fig. 4), caused by the combustion of fossil fuel and deforestation (KEELING *et al.* 1989).

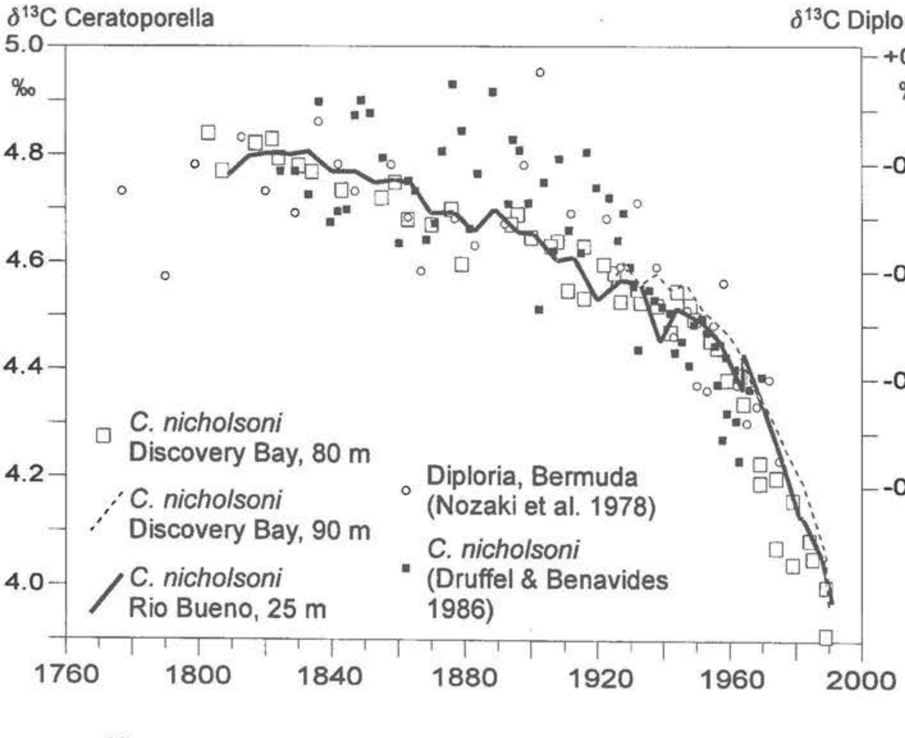

Fig. 3. Comparison of $\delta^{13}C$ records of *C. nicholsoni* (Jamaica) and the coral *Diploria labyrinthiformis* (Bermuda). The coral record (right scale) is shifted by about 5‰ for better comparability. Two of our records (lines) show surprisingly little scatter. All records display a decrease of the same magnitude (about -0.5‰) from preindustrial times until 1970. The accelerating decline of $\delta^{13}C$ has added another -0.3‰ from 1970 to 1990.

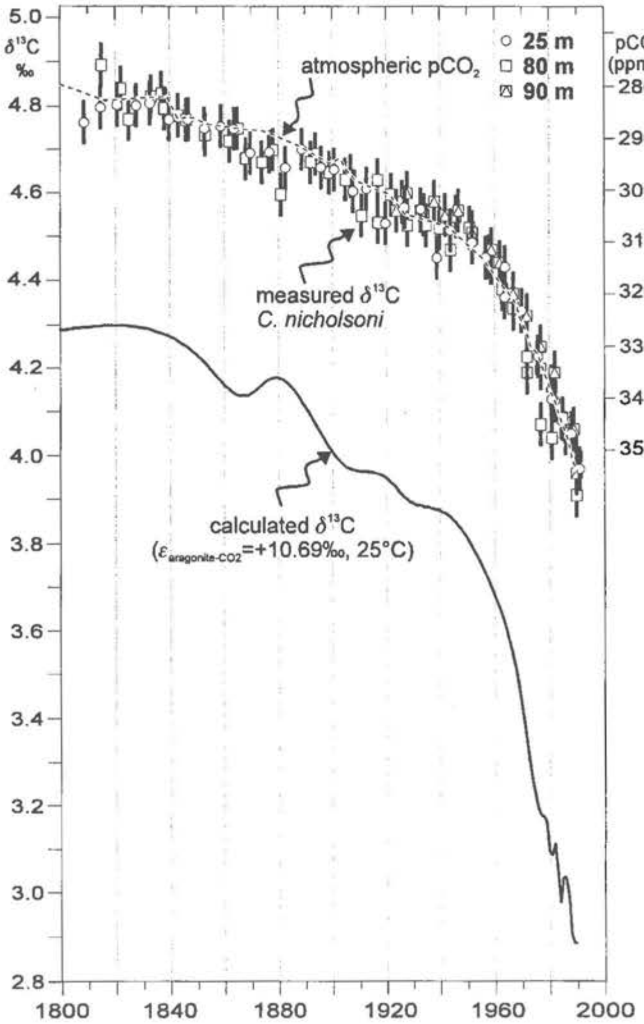

Fig. 4. Comparison between $\delta^{13}C$ of aragonite in isotopic equilibrium with atmospheric CO_2 calculated with the fractionation factor given by ROMANEK *et al.* (1992) and the measured $\delta^{13}C$ of *C. nicholsoni* from Jamaica. Measured preindustrial values (before AD 1830) are about 0.5‰ too heavy compared with the calculated equilibrium values. The disequilibrium increases to 1.1‰ in 1990. Atmospheric pCO_2 (KEELING *et al.* 1989) is shown for comparison (dashed line, right axis), displaying a very good correlation with the measured $\delta^{13}C$ values. Error bars correspond to $\pm 2\sigma$ external precision of $\delta^{13}C$.

It is widely accepted that the oceanic reservoir as a whole was in isotopic steady state with atmospheric CO_2 in pre-industrial times. In order to decipher whether the sponge carbon isotope data support isotopic equilibrium between atmosphere and surface ocean, we calculated the isotopic compositions of CO_2 in isotopic equilibrium with sponge aragonite. We used the fractionation factor $\varepsilon_{aragonite\text{-}CO_2}$ =+10.69±0.62‰ (25°C) determined by ROMANEK *et al.* (1992) and MOOK *et al.* (1974). From 1800 to 1990 the $\delta^{13}C$ values of the sponge aragonite show a depletion of -0.8‰, while the measured atmospheric $\delta^{13}C_{CO_2}$ decreased by about -1.4‰ (KEELING *et al.* 1989, extrapolated to 1990 using data of FRANCEY *et al.* 1995). The difference between calculated and measured isotopic compositions (Fig. 4) increased from +0.5±0.62‰ in 1800 to +1.1±0.62‰ in 1990. Thus, our carbon isotope data measured on Jamaican sponges indicate that (i) atmospheric $\delta^{13}C_{CO2}$ and $\delta^{13}C$ of dissolved inorganic carbon in Caribbean surface waters were probably not in isotopic equilibrium in pre-industrial times and that (ii) this disequilibrium increased by 0.6‰, mostly during the last 30 years (Fig. 4).

The first observation may be an artefact due to the large uncertainty of the fractionation factor. However, local isotopic disequilibrium between surface waters and atmospheric CO_2 is to be expected for most oceanic surface waters (BROECKER & MAIER-REIMER 1992). Our observations were made in an open ocean fore-reef setting. This largely excludes local isotopic modifications, that might affect more restricted settings. Most plausibly, the increase of the isotopic disequilibrium, which started at the beginning of the 19th century, can be explained by the increasing anthropogenic CO_2 release rate and the long isotopic equilibration time of ocean surface waters (BROECKER & PENG 1982; BÖHM *et al.* in prep.).

Our results show that demosponges serve as accurate recorders of long-term isotopic variations in surface water DIC. With that, they can provide data that are necessary to quantify the CO_2 uptake by the ocean reservoir (eg. TANS *et al.* 1993, FRANCEY *et al.* 1995).

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A 50 YEAR-LONG RECORD OF AGULHAS CURRENT VARIABILITY IN CORAL FROM 2-MILE REEF, SOUTH AFRICA

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Abstract - In October 1993, a 43 cm-long coral core was extracted from a large *Porites* dome growing at 2-Mile Reef (27°S, 32°E) off the coast of Zululand, South Africa. The dome is located about 1 km offshore at 16 m depth, bathed by the surface waters of the Agulhas Current. Based on density-band counts, a growth history of 49 years is estimated for this core, spanning the period 1945-1993. Oxygen and carbon isotope values both exhibit strong seasonality but are out of phase. In each annual cycle, the narrow low density band yields highest $\delta^{13}C$ values but does not coincide with either maximum or minimum values of $\delta^{18}O$. Disruption of the annual cycle in $\delta^{13}C$ is apparent in some years but is not matched by a similar disruption in the $\delta^{18}O$ cycle. During these anomalous years, $\delta^{13}C$ values remain depleted throughout the year perhaps indicating a disruption of normal photosynthetic activity. Longer-term trends in the stable isotope records are apparent. The $\delta^{18}O$ record exhibits decadal-scale variability and can be matched with similar scale rainfall trends over the adjacent sub-continent this century. A sea temperature/rainfall relationship is not unexpected in this region but alternative thermometers (e.g. Sr/Ca) are needed to distinguish between salinity and temperature effects in the record. $\delta^{13}C$ values through the 1950's and 1960's are significantly enriched (by about 1°/oo) relative to those of the 1980's and 1990's. The shift was gradual as $\delta^{13}C$ values decreased over a period of about 10 years. Although the $\delta^{13}C$ signal in coral is influenced by both physiological and environmental parameters, it is possible that the longer-term trend in $\delta^{13}C$ apparent in this record is of climatic significance.

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VARIABILITY OF THE OXYGEN ISOTOPIC COMPOSITION OF THREE SCLERACTINIAN GENERA (MAYOTTE, MOZAMBIQUE CHANNEL)

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Abstract - The aim of this study is to point out the variability of oxygen 18 records by different coral genera, as related to some environmental parameters (temperature, salinity and sea water $\delta^{18}O$ values). Three different genera: *Acropora*, *Porites* and *Goniastrea* from different biotopes of the Mayotte lagoon have been analysed. These genera have been chosen because they represent morphologic types very frequent both in modern and fossil reefs.

We compare the $\delta^{18}O$ variations between different growth axes of a single *Porites* colony; between different *Acropora* colonies from different sites; and between 3 genera (*Acropora*, *Porites* and *Goniastrea)* from the same site of the lagoon. This study is characterized by a very high temporal

resolution of approximately 70 points per year in *Acropora,* 20 points per year in *Porites* and about 10 points per year in *Goniastrea.*

The data show that in this specific area $\delta^{18}O$ variations of the coral skeletons essentially record temperature variations.

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SCLEROCHRONOLOGY OF JURASSIC CORALS: GEOLOGICAL APPLICATIONS

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Abstract - Skeletal growth rhythms of Jurassic reef corals have been described as epithecal growth bands and as skeletal density banding in massive and platy scleractinians, and also as regular thinning/thickening of branches in phaceloid and dendroid colonies. Growth rhythms are in the order of less than 1.0 mm to more than 10 mm, depending on systematic position and growth habits of the corals involved.

Skeletal rhythms measured in recent coral species of respective growth forms may approximate these values, but generally, they are notably higher. In recent corals it can be readily shown that rhythms of this order of magnitude are annual in nature (see WAGNER 1994, and others). Hence it is inferred that the growth rhythms observed and measured in the fossil corals are annual too. If this holds true, it provides a uniquely precise timescale enabling us to quantify certain processes of the geological past with a time resolution of less than one year.

Average annual growth rates and the life span of a number of Middle and Upper Jurassic scleractinian colonies have thus been determined by measuring and counting their yearly growth bands. Results show that large massive to platy Bajocian *Isastrea bernardiana* from the eastern Paris Basin commonly attained a life span of more than 100 years with growth increments of 1.0 to 3.0 mm/year. Oxfordian colonies of *Isastrea* sp. of comparable growth habits revealed similar values.

Even faster distal growth rates, of about 10 mm/year, in phaceloid Late Jurassic *Aplosmilia* sp. are indicated by rhythmic thickening of branches. In the quarry of Pagny-sur-Meuse/Lorraine *Aplosmilia* thickets may be 10 or more metres in height (GEISTER & LATHUILIÈRE 1991). Because they baffled sediment continuously during their growth, only the tops of these huge coral thickets rose markedly above the sea floor. The bases were gradually submerged by the rising level of trapped mud. It seems that, at least, some of the thickets are formed by continuous growth of pioneer colonies from the base to the top of the outcrop area. If rhythmic thickening of their branches was annual, as suggested by some recent *Acropora* spp., and vertical growth was continuous as it appears in the outcrop plane, the largest of the *Aplosmilia* colonies must have lived considerably longer than 1000 years. The values of above growth rates and life spans as estimated from massive, platy and branching Jurassic coral skeletons constitute the basis for the following discussion.

Under certain conditions, coral growth rates measured within a fossil reef framework may be used to approximate the accretion rate of an entire reef structure and to estimate the accumulation rates of adjacent sediments. These prerequisite conditions include both biological stability of the reef ecosystem over prolonged growth periods (i.e. the absence of episodic or periodic disruptions of the reef ecosystem by storms or by biological disturbances) and non-significant bioerosion and mechanical break-down of coral skeletons, because these may counterbalance reef accretion. In addition, long lifespans, dense coral growth and fast recruitment of colonies on freshly dead surfaces are neces-

sary to ensure an almost continuous quantifiable reef accretion. Low diversity of frame-builders facilitates these estimates. Under such ideal conditions, we may roughly calculate the average accretion rate and the duration of formation of an entire reef from the known average growth rate of the dominating coral associations.

A carefully studied 18m thick reef body of the Luxembourgian Middle Jurassic (Bajocian) meets the above prerequisites. It was found that the reef represents vertical growth of around 10 000 years, deposited with an average accretion rate of slightly less than 2 mm per year. Adjacent inter-reefal sediments show only negligible onlap. Hence, their deposition rates must have been somewhat lower than the reef accretion rates indicated above (GEISTER 1989). Also, the average rate of sediment-trapping within the coral thickets of the Oxfordian at Pagny-sur-Meuse was close to the approximately 10 mm per year of vertical extension rate measured in adjacent *Aplosmilia* branches (GEISTER & LATHUILIÈRE 1991). However, the sedimentation rate was probably much lower in the coral-free inter-reef sediments outside of the coral thickets than between the corals themselves.

Measuring carbonate production rates in reefs can provide comparative data on carbonate productivity of recent coral species or entire reefs growing in different ecological, latitudinal and bathymetric settings. Annual carbonate production rates of recent and fossil coral colonies may be calculated by multiplying the known vertical annual growth increment of a coral by the real or reconstituted bulk density of its skeleton. Within certain limiting conditions, carbonate production rates of an entire fossil reef may also be calculated from these data and compared to recent reefs. Calculating carbonate production rates of both Bajocian and recent reefs supplies quantitative data on an important, geologically relevant physiological process active in the past and present. It bridges a time lapse of 170 million years of earth history during which this process evolved along with the coral reef ecosystems. During this period the ecosystem underwent considerable changes both gradual and episodic due to the varying composition of the constituting reef coral assemblages. The example of the Bajocian patch reef studied at Luxembourg shows a gross carbonate production rate of $G = 1.6\text{-}1.8 \times 10^3 g/m^2/yr$, thus being at least an order of magnitude below that of recent shallow coral reefs growing under sub-optimal to optimal conditions. This divergence is attributed both to the lack of rapidly calcifying branching coral species in the Bajocian reef and a position somewhat deeper on the shelf as compared to studied recent reefs. In addition, the Luxembourg reef thrived in a somewhat marginal position in respect to the Bajocian tropical belt (GEISTER 1989).

Both Quaternary and Mesozoic reefs grew during eustatic sealevel fluctuations. Lowstand reefs grew during eustatic sealevel lowering and at lowstands in rather deeper basinal and shelf settings. They became established on top of sediments deposited during the previous highstand. Together with these underlying sediments they may record a substantial part if not the whole of the depositional cycle, especially if deposited in a subsiding basin. Highstand reefs, by contrast, formed in late phases of eustatic transgressions on a freshly submerged substrate in a topographic high coastal position. They can record only part of the highstand event and are also subject to major subaerial and intertidal erosion during the sealevel lowering of the subsequent cycle. In the more complete record of the lowstand reefs we may occasionally recognize a well-defined, large segment of the total rise and fall of sealevel. If the age of this segment can be quantified sclerochronologically in years, we may roughly estimate, by extrapolation, the duration of the entire eustatic cycle.

The top of the Bajocian reef at Luxembourg is truncated by a synsedimentary hardground. What is left of the sequence appears to be half, if not almost the whole, shallowing-upward segment of the sedimentary column formed in about 10'000 years. If this estimate is realistic, the preserved part of the fossil reef would equal a quarter to a half of a supposed sinusoidal eustatic cycle. The reconstituted complete eustatic cycle, accordingly, must have had a minimum duration in the order of 20'000 to 40'000 years. Even if the reef body would represent a somewhat smaller fraction of the eustatic cycle, it would easily fall within the limits of the Milankovitch periodicities of wave-length (ranging from 20'000 to 400'000 years) which were recognized in Quaternary deposits.

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FLUORESCENT GROWTH BANDS IN CORALS FROM MURUROA ATOLL

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Abstract - 3 *Porites* spp. corals were collected on the inner reef slope of Mururoa atoll (Tuamotu Archipelago, French Polynesia). Density bands were studied on X-radiographs and compared to fluorescent bands revealed by ultra-violet light on both sides of ca 4 mm thick coral slabs.

Skeletal density banding on X-radiographs was rather indistinct, and its annual pattern was further obscured by fine banding and by growth of endolithic green algae. In reference to the collection time (June 1993), skeleton high density (HD) was apparently accreted during the cold season and skeleton low density (LD) during the warm season.

Apart from a single narrow yellow fluorescent band, at 2-3 mm under the surface of the skeleton, due to the presence of the familiar brown layer of endolithic algae visible in daylight, fluorescent banding showed a well defined major rhythm in all colonies. Couplets of beige/purple bands which corresponded to LD/HD scleroband couplets suggested growth rates of about 2.1 cm/yr. Beige bands were the wider (about 1.3 cm) and matched LD bands. Purple bands, about 0.8 cm wide, matched HD bands. A second rhythm of finer fluorescent bands was superimposed on the major rhythm. This was composed of fine beige bands 1 to 2 mm wide, alternating with purple bands up to 4 mm wide. A grouping of 3 to 5 fine beige bands resulted in a major beige band. These fine fluorescent bands did not match skeletal density bands.

Up to now fluorescent bands in corals growing near mainland coasts have been described as a signature of terrestrial run-off due to fulvic acids incorporated in their skeletons. At Mururoa there may be sufficient organic compounds to cause fluorescence in coral skeletons from the thin soils of the motus. Fluorescent banding was also present in corals coming from other atolls: Tikehau, Takapoto (Tuamotu Archipelago), and Scilly (Society Archipelago). All *Porites* colonies collected from sand cay reefs did show fluorescent bands: the cay being either permanently emerged (Tromelin), or submerged at high tide (Geyser Bank). Furthermore, *Porites* coming from Leven Bank and La Zélée Bank, submerged at 13 m and 20 m depth respectively, did also reveal fluorescent banding. This showed that the origin of the fluorescent banding recorded in these coral skeletons is certainly not from terrestrial origin. This study indicates that fluorescent banding may be ascribed to endolithic algae alone.

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CORAL CORES FROM THE COMORO ISLANDS

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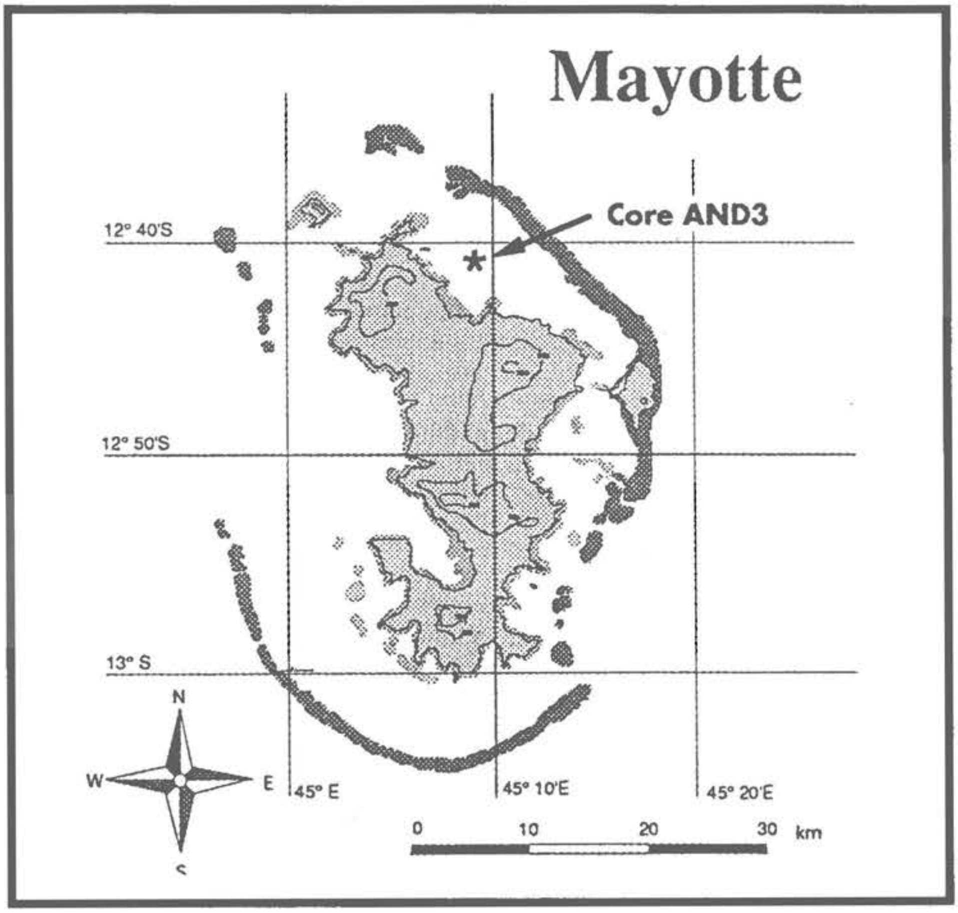
Abstract - Several cores were drilled into massive colonies of *Porites* at Mayotte, Comoro Islands, Indian Ocean (13°S, 45°E). The volcanic island of Mayotte is surrounded by a broad barrier reef. The cores were taken from corals situated in the lagoon, in a passage and on the outer reef.

Growth rates, skeletal carbon and oxygen stable isotopes were measured for the longest core (AND3, 238 cm) taken at two meters water depth in the lagoon. These results represent the first long-term isotope profiles for corals from the tropical Indian Ocean.

Implications for palaeoclimatic reconstructions (sea water temperature, salinity) and carbonate production will be discussed. The results will be compared to previous studies from the Red Sea.



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GROWTH BANDING IN TWO JURASSIC CORALS: REGIONAL AND LOCAL VARIATIONS

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Abstract - A Pan-European sclerochronological study was carried out on two Jurassic corals, *Thamnasteria concinna* (Goldfuss) and *Isastraea explanata* (Goldfuss). The aim of the study was firstly to identify the controls on the deposition of growth bands, on both a regional and local scale, and secondly to assess the potential value of Mesozoic sclerochronology as a tool for palaeoenvironmental and palaeoclimatic interpretations. The growth bands of these two corals were compared in two situations: (1) between different geographic regions (extending from the Swiss Jura through to Yorkshire), within the same reef type; (2) between different reef types such as deep and shallow-water reefs, within the same region.

The results indicate that *Isastraea explanata* was the faster growing of the two species with growth rates reaching 4.0mm/yr where conditions were optimal for coral growth (as compared to 2.8mm/yr for *Thamnasteria concinna* in the same environment). In deep-water reefs growth rates of both corals were considerably lower. This reduction in growth rate is accompanied by a change in growth form from dome-shaped colonies in shallow-water to plate-shaped forms in deeper water. Both the reduction in growth rate and change in growth form are interpreted as a response to a reduction in light availability in the deep-water reefs. *Thamnasteria concinna* showed a substantially greater variability in its growth rate between different environments (up to 50% of its optimal growth rate).

Low/high density band ratios do not show systematic variations between different regions or between the two species. L/H values were greatest in shallow-water and decreased significantly in deeper water (the high density portion of the growth couplet increased in width, whilst the low density band remained the same size). However, where reef development coincides with areas of high siliciclastic influx L/H ratios, even in shallow-water reef, were low as a result of the increased local turbidity.

The distinctness of the bands was found to be only indirectly related to seasonality - through increasing seasonal run-off to reef areas. Where there was no influence of landmasses the effects of seasonality seemed to be less pronounced and consequently the distinctness of the bands is less marked. The high distinctness values recorded in all the regions suggest that central Europe experienced a highly seasonal climate during the Late Jurassic.

No regional patterns in either the nature of the growth bands or the growth rates were revealed by the data. It is suggested that this reflects the more equitable Jurassic climate and hence less steep environmental gradients. Growth rate data are needed from localities closer to the Jurassic palaeoequator and from high palaeolatitudes (greater than 40°N) to assess fully the influence of climatic variations on Mesozoic coral growth bands. However all the results of this preliminary study are consistent with studies carried out on the growth patterns on present day corals. The study illustrates that the concepts, models and methodology developed for present day sclerochronology can be successfully applied to Mesozoic corals and provides a valuable tool for palaeoenvironmental and palaeoclimatic interpretations.

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STABLE ISOTOPIC RECORD FROM A RED SEA CORAL

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Abstract - Reliable global records of palaeoenvironmental data need to be established in order to understand and predict climate variability. Surprisingly, the number of records from dry regions of the world is limited. Among the best proxy records of past climate change over the past several centuries are the annual growth bands of scleractinian corals. Here we present an oxygen isotope time series from an 88 years (1906-1993) coral core drilled in massive *Porites* from the reefs of the southern Sinai, Red Sea. Average summer and winter values were measured by sampling high and low density bands. The data show interannual anomalies of the stable oxygen isotopes with marked heavy signals at the turn of this century. This indicates a cooling of the surface seawater during this period and suggests colder climate prevailing in the Sinai at the beginning of the century. A temperature rise can be reconstructed from 1906 to 1924. Since then decadal time scale variations in oxygen isotopes are observed. The oxygen isotopic record from the Sinai coral shows some similarity with the land air temperature record of the northern hemisphere, and with a regional dendrochronological data set.

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THE RATIO Sr/Ca IN THE CORALLINE SKELETON: PALAEOTHERMOMETER OF SEA SURFACE WATER OF THE OCEAN

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Abstract - Sr/Ca ratios of aragonite corals have been increasingly used as a palaeothermometer of Surface Sea Water, in recent years. We analyzed massif hermatypic corals (*Diploria strigosa, Montastrea cavernosa* and *Porites lobata*) from Bermuda and Philippines, in order to refine the Sr/Ca-δ^{18}O-temperature calibrations. Sinusoidal seasonal variations of Sr/Ca are observed for *Diploria strigosa* and *Montastrea cavernosa*, correlated to density variations and δ^{18}O oscillations. The slopes of the δ^{18}O-Sr/Ca and Sr/Ca/temperature correlations are respectively 2900 and 21470 for *D. strigosa*. This slope is close to the thermodynamic value 25640. On the other hand this value is slightly different from those obtained by previous studies, depending on species and environment.

In order to test kinetic effects linked to calcification rate, we analyzed synchronous growth bands from one head of *Porites lobata* from the Philippines, álong two transects with different extension rates. We obtained a significant shift between the two profiles for Sr/Ca (0,0718 mmol/mol during cold season and 0,111 mmol/mol during warm season) and δ^{13}C (-2,337 °/oo), whereas δ^{18}O remains relatively similar on the two profiles. These results are in agreement with those reported recently by De VILLIER *et al.*

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SKELETAL CORRELATES OF CORAL DENSITY BANDING AND AN EVALUATION OF RADIOGRAPHY AS USED IN SCLEROCHRONOLOGY

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Abstract - Studies on growth patterns in contemporary corals have centred on the observation of alternating dark (= high density) and light (= low density) bands on radiographs taken of slices of coral skeleton. Couplets of dark and light bands have been shown to reflect seasonal variations in the apparent bulk density of skeleton. Density banding is considered a characteristic feature of massive coral skeletons, and banding patterns have the potential to provide a marine analogue to dendrochronology and dendroclimatology. Studies on density band patterns in corals have been principally concerned with the pursuit of empirical linkages with environmental parameters. In contrast, little effort has been directed towards determining how variations in coral skeleton architecture cause banding patterns, and radiographs have been regarded as direct photographic illustrations of skeletal structure and density. Using the massive Indo-Pacific coral *Porites lutea* and the branching Caribbean coral *Porites porites* two aspects of radiography have been investigated, (1) the skeletal correlates of density band patterns, and (2) possible sources of error in constructing chronologies using banding patterns. The results have shown that radiography resolves finer detail of the coral skeleton than has been previously recognized. Small changes in path length of individual skeletal elements attenuating an X-ray beam, including dissepiments as thin as 3 - 10 µm, can generate contrast on radiographs as well as variations in skeletal bulk density. The annual high/low density band pattern was found to be correlated with areas of relatively thick/thin skeletal elements respectively. Secondary density variations seen on radiographs, 'fine' bands', were found to be correlated with the position of corallite walls oriented perpendicular to the long axis of the skeletal slice or dissepiments. Modelling of skeletal slices showed that errors in the density band record may be introduced by (i) skeletal slices not following the growth axis of the colony, and (ii) changes in corallite orientation which generate density variations that are not part of any growth record. The use of radiography as a tool for demonstrating growth records in coral skeletons is critically reviewed. It is proposed that the skeletal growth record consists of patterns of thickening/thinning and spacing of skeletal elements. Illustrations of these patterns by analysis of the actual skeleton, rather than by radiography, may prove to be a very accurate method of determining growth records in corals.

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LINEAR SKELETAL EXTENSION RATES IN *Diploria labyrinthiformis* FROM BERMUDA OVER THE LAST 30 YEARS

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Abstract - Mean annual linear skeletal extension (growth) rates in the reef-building coral *Diploria labyrinthiformis* (L.) have been studied from the high-latitude reefs of Bermuda, mainly by X-radiography. Colonies were obtained from 8 localities representing various biotopes across the Bermuda platform and band couplets measured and dated, to produce index master chronologies of mean and maximum growth rates for each locality and for Bermuda as a whole. Growth rates are highest and most variable in shallow inshore, nearshore and lagoonal waters, decreasing towards the edge of the Bermuda platform and with increasing depth beyond the platform margin. There is a steady increase in growth rates for this species, for most localities and for Bermuda as a whole, from about 1966 to 1975, after which they stabilized. Possible factors influencing this trend include eutrophication of platform waters, fluctuations in air and sea temperatures and perhaps others, as yet unknown.

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THE BERMUDA CORAL PROXY RECORD

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Abstract - Different species of *Diploria* and *Montastrea* from the Bermuda Islands were studied for annual growth rate patterns, stable oxygen and stable carbon isotopic composition. The coral proxy records were compared with climatological data sets from the Bermudas, with the instrument record of the Hydrographic Station S in the Sargasso Sea, and the COADS data set. Annual growth rate patterns of Bermuda corals show an inverse correlation with average annual sea surface temperatures which seems to be linked to the annual pattern of vertical mixing of the surface water column and the supply of nutrients. High resolution profiles of seasonal stable oxygen isotopic composition along growth direction reflect the seasonal SST variations and average annual oxygen isotopic data keep track of temperature changes during the last centuries. Seasonal carbon isotope variations are linked to the seasonal carbon cycle of the water column and the coral-algae symbiotic relationships. Long term trends of carbon isotope proxy records still remain a matter of controversial interpretations.

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SCLEROCHRONOLOGY OF RUDIST-BIVALVES

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Abstract - During the Cretaceous, rudist-bivalves occupied shallow marine environments which were dominated by coral-algal communities before and after this period. An invaginated or even missing ligament enabled this peculiar group of inequivalve molluscs to flexible, upwardly directed shell growth. Knowledge of growth rates and environmental demands are, therefore, particularly important to understand their spectacular success in Late Cretaceous sublittoral environments. Relevant information is stored in the structures, isotopic, and elemental compositions of their shells. The Hippuritidae and compact-shelled Radiolitidae proved to be well suited for sclerochronological analyses because their massive outer shell layer was built of diagenetically stable low-Mg calcite. Results of several specimens of *Vaccinites cornuvaccinum* (Bronn), a compact-shelled *Gorjanovicia* cf. *costata* Polšak, and a *Torreites sanchezi* (Douvillé) will be presented.

Recent bivalves are known to record seasonal variations of temperature and isotopic composition of sea water rather faithfully, as they precipitate calcite largely in isotopic equilibrium with ambient water. This seems to be the case for *V. cornuvaccinum* and *G.* cf. *costata*. Cyclic shifts of d^{18}O within their shells are related to seasonal variations of temperature. The resulting palaeotemperatures are reasonable but their interpretation is hampered by uncertainties about the d^{18}O of Cretaceous seawater. Additionally, evaporation or influx of fresh water might have modified the isotopic composition of their environments to a certain extent, although rudist-bivalves are considered to be strictly stenohaline. Annual growth increments are deduced from the observed cyclicity in d^{18}O and amount to 30-40mm in juvenile hippuritids and usually decrease to 10-15mm in adult growth stages. Maximum vertical growth rates of 50mm per year were determined for *G.* cf. *costata*.

In several shells of *V. cornuvaccinum*, decelerated growth during the warm season is indicated by patterns of the d^{18}O curves, dark growth lines, and modifications of the fibrous-prismatic ultrastructures of the shells. By comparison with reported growth patterns of extant bivalves, this is assumed to reflect annual periods of reproduction.

Mg-, Sr-, Mn-, and Fe-concentrations within the shells are similar to those of recent bivalves. The sclerochronological distribution of Mg revealed cyclic variations which are correlated with those of d^{18}O.

The isotopic composition of the shell of *Torreites sanchezi* was apparently ruled by kinetic isotope effects, as known from ahermatypic and hermatypic corals. Although d^{18}O cannot be related to seasonal temperature variations, second order cycles correspond to dark growth lines and are assumed to reflect annual growth patterns.

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ENVIRONMENTAL CHANGE AND DEGRADATION IN ANCIENT AND RECENT REEFS

PATHOLOGIC SYNDROMES ON REEF CORALS : A REVIEW

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Abstract - Pathologic syndromes on reef corals fall into two distinct categories : diseases without, and diseases with pathogens. In the first group, no pathogen is involved in the progress of the disease, but the pathologic condition (or reaction) is caused or triggered by outside influences. This is the case in Tissue Bleaching (TBL), Shut-Down-Reaction (SDR), and White Band Disease (WBD). In the second group, progress of the disease depends on the presence of a distinct pathogen. This group includes Black Band Disease (BBD), Black Overgrowing Cyanophyta (BOC), Black Aggressive Band (BAB), Bacterial Infection (BIN), and Fungal Infection (FIN). A newly discovered, lethal syndrome on reef-building coralline algae is included.

1. INTRODUCTION

Coral pathology may be the smallest and slowest-growing sidebranch of coral reef science. First observations on pathologic syndromes were made two decades ago (ANTONIUS 1973), and the last review dates back more than ten years (ANTONIUS 1981a). Since then our understanding of the pathogenesis of some known diseases, especially White Band Disease (WBD) and Black Band Disease (BBD), has increased considerably, and several new syndromes can be added here. Besides WBD and BBD, the old list also contained Bacterial Infection (BIN) and Shut-Down-Reaction (SDR). The new syndromes are the so-called Coral Bleaching or Tissue Bleaching (TBL) that has made recent headlines (*e.g.* Coral Reefs, vol.8, no.4, 1990), and the less well-known phenomenon of Black Overgrowing Cyanophyta (BOC), which was first reported only last year (ANTONIUS 1993). The Black Aggressive Band (BAB) is listed here, but has not yet been investigated (ANTONIUS 1993). Another relatively new disease is Fungal Infection (FIN) of reef corals (RAGUKHUMAR & RAGUKHUMAR 1991). Not excluded from this list should be a most recently discovered lethal orange disease on reef-building coralline algae (LITTLER & LITTLER 1994), for which the abbreviation "LOD" may be proposed.

2. DISEASES WITHOUT PATHOGEN

All syndromes listed in this chapter have in common the lack of a pathogen in the progress of the disease. The pathologic condition of the coral is caused by environmental circumstances or is triggered by some biological agent. This group of syndromes, i.e. Tissue Bleaching (TBL), Shut-Down-Reaction (SDR), and White Band Disease (WBD), has also been lumped under the term White Syndromes (WS) previously (ANTONIUS 1988a).

2.1. Tissue Bleaching

Coral Bleaching or Tissue Bleaching (TBL) has occupied the scientific community for over a decade. Early reports on TBL in Panama (GLYNN 1983) were followed by observations in the Caribbean (WILLIAMS *et al.* 1987) and culminated in a special issue of Coral Reefs (BROWN 1990) containing eleven contributions devoted to coral bleaching. The term "bleaching" refers to a loss of colour of the coral tissue, brought about by a reduction in the number of zooxanthellae, by a loss of photosynthetic pigment, or by a combination of both.

Most evidence points to elevated water temperatures as the main cause of bleaching. Some of these events were linked to oscillations of seasonal winds known as "El Niño" (GLYNN 1984). El Niño-related seawater warming was observed at geographic locations as distant as Panama (GLYNN 1983) and Indonesia (BROWN & SUHARSONO 1990). These events were usually shallow-water phenomena. TBL in deeper water, without perceptible temperature changes, remains largely unexplained. The general rise in the atmospheric CO_2-concentration is one suspect (PECHEUX, this volume), while my own observations indicate industrial seawater contamination and simple freshwater-runoff as further possible culprits (ANTONIUS 1988a). RIEGL (1995) showed sedimentation stress to result in tissue bleaching and necrosis in soft corals. TBL is not necessarily lethal, and corals are usually able to recover their symbionts once environmental conditions return to normal. However, for the duration of the bleaching event, tissue biomass, growth rate, and reproduction rate are all negatively affected (SZMANT & GASSMANN 1990), and, if the event lasts long enough, this condition may eventually lead to the death of the specimen or even to the demise of entire sections of a reef tract.

2.2. Shut-Down-Reaction

A continuing stress on a coral may not in itself kill the animal, but still lead to a catastrophe. Aquarium experiments and field observations have shown that corals which are under sublethal stress (*e.g.* temperature, sedimentation, chemical pollution) but have not yet begun to bleach, can die from a rather harmless additional impact that would never damage a healthy coral. A simple scratch on the coral surface, for instance, can trigger a syndrome that kills corals so rapidly that it was named the Shut-Down-Reaction or SDR (ANTONIUS 1977).

The process can only be described as a complete, sudden disintegration of the coral tissue, starting at the margins of the injury. The coenosarc sloughs off the skeleton in thick strands or blobs, leaving behind a completely denuded coral skeleton with no trace of tissue. From the initial interface, the phenomenon proceeds in an enlarging circle on massive corals, or moves along the branches in ramose forms, spreading to all side-branches upon reaching a junction. The speed of the process is about

10cm per hour, fast enough to be visually observed. What makes SDR especially dangerous is its extreme contagiousness. SDR can be transmitted by contact to neighbouring colonies which are themselves under stress; they only have to be touched by a floating strand of dissolving, contaminated tissue to produce the onset of SDR. Thus, in a coral reef under a certain degree of stress, SDR could well start a catastrophic chain reaction (ANTONIUS 1981a).

2.3. White Band Disease

The third coral disease without a pathogen is White Band Disease (WBD). The name refers to a band of white coral skeleton, which is always visible in the wake of a moving front of tissue destruction. This front is a simple interface across a coral colony, advancing at a rate of a few millimetres per day. WBD was first observed in the Caribbean Sea on *Acropora palmata* (GLADFELTER *et al.* 1977) and several other coral species (ANTONIUS 1981b), but was later reported to occur throughout the Indo-Pacific on a wide variety of scleractinians (ANTONIUS 1984; 1985a; 1988a).

Years of observation have revealed WBD to be triggered by blue-green algae which are apparently toxic to corals. This is why WBD always starts at a point or a line where coral tissue touches benthic overgrowth. Where this epibenthos is green, composed mainly of Chlorophyta, nothing happens. Where the algal turf is dark, containing Cyanophyta, it may trigger WBD (ANTONIUS 1981a; 1985a).

3. DISEASES WITH A PATHOGEN

This chapter lists all syndromes in which the progress of the disease is dependent on the presence of a distinct pathogen. So far, Black Band Disease (BBD) has been described exhaustively (see references in ANTONIUS 1988b), while Black Overgrowing Cyanophyta (BOC) and Black Aggressive Band (BAB) have only been mentioned once (ANTONIUS 1993). Since the pathogen in these diseases is usually visible as a dark band or dark overgrowth, the term Black Syndromes (BS) coined earlier (ANTONIUS 1988a) may be applicable to all three. Bacterial Infection (BIN) is known for some time (MITCHELL & CHET 1975), but Fungal Infection (FIN) is a rather recent observation (RAGHUKUMAR & RAGHUKUMAR 1991) which also belongs into the BS-group. A Lethal Orange Disease (LOD) on reef-building coralline algae is certainly the newest discovery in this field (LITTLER & LITTLER 1994).

3.1. Black Band Disease

BBD is probably the best-known of all coral diseases (*e.g.* ANTONIUS 1981a; 1985a; 1985b; 1988b). Caused by the cyanophyte *Phormidium corallyticum*, it was discovered in the Caribbean Sea (ANTONIUS 1973), but has been shown meanwhile to occur in many parts of the Indo-Pacific as well (ANTONIUS 1985a; 1988b). In the Caribbean, it is most often found on *Diploria strigosa* and *Montastrea annularis*, but also occurs on other scleractinian species as well as on Gorgonia (ANTONIUS 1981b). In the Indo-Pacific, there are very interesting geographic differences in occurrence of BBD on different species (ANTONIUS 1988b). For instance, *Goniastrea retiformis* is one of the most susceptible species in the Red Sea, belonging to the "Susceptible Fast" (F) group of possible susceptibilities (ANTONIUS 1988b). In Papua New Guinea, *G. retiformis* proved to be rather immune to the disease, fitting here the characteristics of the "Immune" (I) group. In this zoogeographic region, BBD was also tested on the octocoral *Heliopora coerulea*. The results indicate that *H. coerulea* can be artificially infected, but with minimal success; this would put *H. coerulea* into the same "Resistant" (R) group as, for instance, *Millepora* (for presently available information on species-specific susceptibility to BBD, see ANTONIUS 1988b).

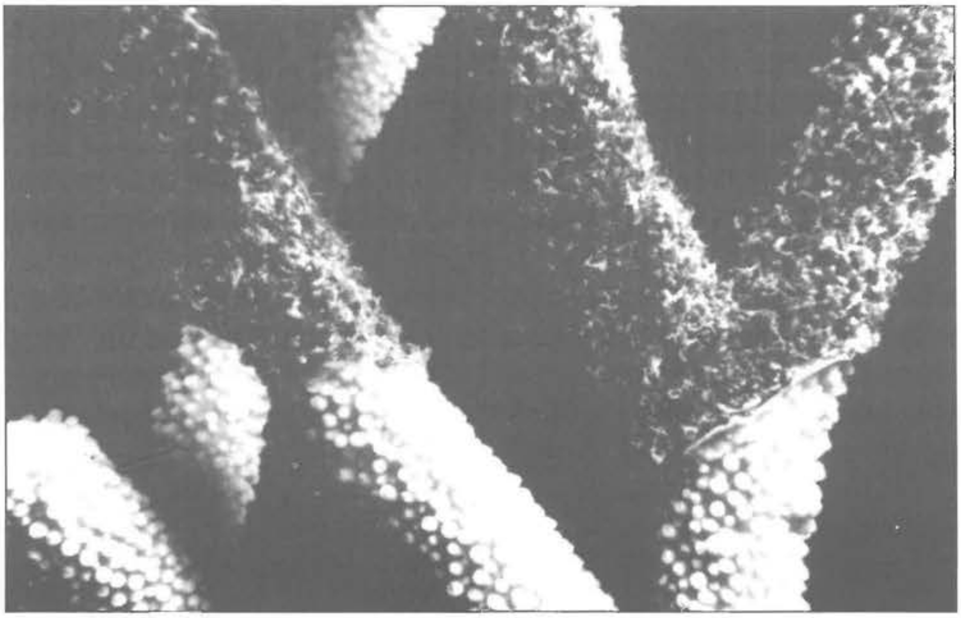
BBD establishes itself when microscopic algal filaments (trichomes) of the pathogen settle on corals under very specific circumstances (ANTONIUS 1981b; 1985a; b; 1988b). The first tiny algal speck soon grows, and turns into an algal ring around a centre of tissue-stripped coral skeleton. The BBD, now firmly established, advances several centimetres a week, killing more and more coral tissue, thus constantly enlarging the area of denuded skeleton. Small corals, depending on size, are killed in a few days to a few weeks. On larger colonies, the infections have a tendency to disappear after a similar period of time, mainly because the algal pathogen is lacking sufficient light on the vertical sides of these corals (ANTONIUS 1981b).

3.2. Black Overgrowing Cyanophyta

It appears that corals can be killed by a variety of other blue-green algae in a less specialised manner. Mainly in the Indian Ocean, I have investigated Black Overgrowing Cyanophyta (BOC) on staghorn *Acropora* (figure 1, 2), *Pocillopora,* branching and massive *Porites, Favia stelligera,* and on many others (ANTONIUS 1991; 1993). These BOC-covers sometimes simply overgrow the coral - and thereby kill it - without actually preying on it, such as a true BBD does. On the other hand, BOC often actively penetrates and erodes the coral skeleton, eventually leading to structural collapse of the corallum. BOC can also trigger WBD with all its consequences.

Fig. 1. (left). Typical BOC cover on the branch-tips of staghorn *Acropora*. The lower (white) parts of the colony are alive.
(Both photos: E. Ballesteros).

Fig. 2. (below). Close-up of a BOC infection on *Acropa sp.* On the right branch, the desease visibly competes against coral regrowth. Note the skeletal lip-formation at the interface.



Quite a number of cyanophytic species were isolated in these BOC covers, including *Calothrix crustacea, C. scopulorum, Hormothamnium solutum, Lyngbia confervoides, L. semiplena, Phormidium spongeliae,* and *Spirulina subtilissima* (ANTONIUS 1993; BALLESTEROS in press). Field observations have clearly revealed what such BOC covers can do to corals. Still missing are controlled aquarium experiments determining the specific role of the different algal species involved.

3.3. Black Aggressive Band

This new disease, tentatively and neutrally termed Black Aggressive Band (BAB), was discovered on staghorn *Acropora* during a survey in Mauritius (ANTONIUS 1991; 1993). *In situ,* it resembles true BBD, but the band material is thinner and appears grey rather than black. Under the microscope, BAB is composed of densely packed, black micro-dots, with the white coral skeleton shining through; it thus appears grey to the unaided eye.

Under fieldwork conditions it was not possible to fully analyse the nature of the pathogen. Our initial diagnosis was a species of the cyanophyte *Spirulina,* but closer examination of preserved material in the lab opened the possibility that it could even be a spirochete (BALLESTEROS, pers. comm.). BAB was found in a shallow lagoon, close to the effluent of a sugar mill. Chemical analysis showed an abnormally high phosphate content of the seawater, so there is reason to assume that BAB is promoted by phosphorus.

3.4. Bacterial Infection

The main defence of corals against all kinds of attacks or irritations is mucus production. That this defence works well, even against BBD attacks, has been proven in experiments (ANTONIUS 1981b). But sometimes it can lead to an unwanted effect, since the mucus, being a glycopeptide, attracts bacteria. Once Bacterial Infection (BIN) has taken place and bacteria form a web-like film over the layer of mucus, only a strong current, washing away the infected slime, can save the coral. Otherwise, a complicated succession of predatory bacteria uses the mucus as a source of carbon and nitrogen, resulting in a tremendous rate of microbial activity. Dissolved oxygen concentration at the coral surface is soon reduced to zero, and within a few days the coral dies (MITCHELL & CHET 1975). At the final stages, the microbial mix is always dominated by *Desulfovibrio* and *Beggiatoa* species (ANTONIUS 1981a).

3.5. Fungal Infection

Fungal Infections on reef corals seem to differ considerably in virulence. A lower phycomycetous fungus, associated with BBD in the star coral *Montastraea annularis* (RAMOS-FLORES 1983) is probably a secondary invader (ANTONIUS 1984). BAK

& LAANE (1987) have shown the association of an ascomycetous fungus with annual black bands in reef coral skeletons.

In the Andaman Islands, a hyphomycetous fungus, *Scolecobasidium* sp., was found in necrotic patches of corals not suffering from BBD (RAGHUKUMAR & RAGHUKUMAR 1991), and for this particular disease the abbreviation "FIN" is used here. FIN-afflicted coral species are either massive or platy, such as *Porites lutea, Goniastrea sp., Goniopora sp.,* and *Montipora tuberculosa,* but never branching. Sections reveal a zonation of organisms: the top layer of the necrotic patch is overgrown with epilithic algae, sometimes intermingled with fungus. This is followed by a thin zone of fungal growth, giving way to a green band containing shell-boring algae. Beneath this is always a dense layer of fungal growth. The fungal zones above and below the green band appear brown to black, with a width of 0.5-1.5cm. Dense fungal growth is found around certain corallites, with the fungus even passing through these into deeper parts of the coral skeleton (RAGHUKUMAR & RAGHUKUMAR 1991).

There does not seem to be any pollution responsible for FIN occurrence in the Andaman Islands, but siltation is suspected to play a role. Primary infections with *Scolecobasidium sp.* are thought to be facilitated through wounds caused by boring organisms. Entry of the pathogen might be followed by growth and ramification of the fungus in the coral tissue resulting in subsequent polyp death (RAGHUKUMAR & RAGHUKUMAR 1991).

3.6. Lethal Orange Disease

A Lethal Orange Disease (LOD), consuming the reef-building coralline alga *Porolithon onkodes* was discovered very recently (LITTLER & LITTLER 1994) on Aitutaki Atoll, Cook Islands. It is included here because reef-building coralline algae, particularly *P. oncodes* in the Pacific, are the principal cementing agents that maintain the reef crest (LITTLER & DOTY 1975). This intertidal wave-resistant reef crest is the main protection of many shallow-water reef communities and beaches (NUNN 1993). The discovery that *P. onkodes* can be destroyed by LOD, caused by an as yet undescribed bacterial pathogen, should be cause for considerable concern (LITTLER & LITTLER 1994).

4. OTHER BIODESTRUCTION

Coral biodestruction not caused by diseases is nevertheless usually included in the record of reef surveys (ANTONIUS 1994). Thus, a listing is given here for the sake of completeness.

Various organisms were observed to overgrow living scleractinians under certain circumstances. These are: the brown alga *Lobophora variegata* (ANTONIUS 1991, 1993); the sponge *Terpios hoshinota* (ANTONIUS 1993); the zoanthid *Palythoa* sp. and the octocoral *Erythropodium caribaeorum* (ANTONIUS 1977); also colonial ascidians of the family *Didemnidae* (ANTONIUS 1993).

Predators on reef corals are: the polychaete *Hermodice carunculata* (ANTONIUS 1973); gastropods of the genera *Turbo, Drupella,* and *Cyphoma*, as well as several seastars, the most destructive of which is the "crown-of-thorns" *Acanthaster planci* (ANTONIUS 1971).

5. CONCLUSION

All the diseases and pathologic syndromes or reactions dealt with here occur under natural conditions. Phylogenetically, they are probably almost as old as coral reefs themselves, and there is every reason to assume that reefs are adapted to the steady toll they take. Thus, diseases do not seem to pose a threat to healthy reefs. Anthropogenic influences, however, drastically alter this scenario. All the typical man-made stresses, such as chemical pollution, thermal pollution, sedimentation, and direct physical impact (dredging, blasting, boat-anchors, divers, etc.), exert a remarkable destructive pressure of their own. In addition, they also considerably enhance the effect of natural diseases. Thus, any kind of pollution will increase the incidence of BIN. Under conditions of eutrophication BBD will flourish and destroy coral species which are immune to the disease under normal conditions; this effect also holds true for WBD. Eutrophication also enormously enhances the occurrence of BOC, which in turn can trigger WBD. Under various combinations of circumstances, TBL will occur, and under very poor conditions, SDR will be triggered.. Thus, under man's influence, the same natural diseases are still at work, but in such an increased frequency that the reefs may no longer be able to cope. There can be no doubt that the gravest threat to coral reefs in modern times are the synergistic effects of man-made stresses and natural diseases.

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IMPACTS ANTHROPIQUES SUR LES ÉCOSYSTÈMES RÉCIFAUX ET CÔTIERS DE L'ÎLE MAURICE (SW OCÉAN INDIEN) : LES ÉLÉMENTS NUTRITIFS DANS LES EAUX INSULAIRES ET LES LAGONS DE 1989 À 1991.

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Résumé - Des signes de dégradation des coraux ayant été observés à l' île Maurice en 1987, un projet d' étude a été organisé par la Commission des Communautés Européennes puis repris par le Fonds National Suisse de la Recherche Scientifique pour mettre en évidence les impacts anthropiques sur les écosystèmes récifaux.

L' origine des éléments nutritifs présents dans les lagons n' est pas océanique. Tous les lagons dont les teneurs en éléments nutritifs sont élevées se situent en aval des régions insulaires les plus polluées, dans la zone de Port-Louis, dans celle de Trou d'Eau Douce, dans le Sud et dans le Nord de l' île.
La présence de phosphates dans les eaux insulaires est liée aux cultures maraîchères, aux élevages, aux industries textiles et sucrières. La présence de nitrates est toujours liée à la nature du couvert végétal. L' origine de la silice est en grande part naturelle et les concentrations évoluent en fonction de la nature des sols traversés par les rivières.

Les nitrates sont toujours plus concentrés dans les nappes phréatiques que dans les eaux de surface. L' impact des eaux souterraines sur l' écosystème récifal est donc plus important que celui des eaux de surface.

Les récifs les plus dégradés se rencontrent dans les zones où les teneurs en éléments nutritifs sont les plus élevées, c' est-à-dire sur les pentes externes soumises à l' influence des panaches de Tamarin et de Trou d' Eau Douce et dans les 4 premiers mètres d' eau de la baie de Trou d' Eau Douce qui sont riches en éléments nutritifs.

La dégradation des coraux de l' île Maurice résulte d' un déséquilibre général du milieu récifal causé par les activités anthropiques, par les apports insulaires importants et par la pêche intensive qui a dépeuplé les lagons.

Abstract -Indications of coral damage were observed in 1987 at Mauritius island. A project to study the anthropogenic impact upon the reef ecosystems was established by the European Community and then taken over by the Swiss National Science Foundation.

The origin of the nutrients found in the lagoons is not oceanic. All the lagoons with high nutrient contents are found downstream from the most polluted parts of the island, in the region of Port-Louis, in the region of "Trou d' Eau Douce" in the South and in the North.
The phosphate content of the island water is linked with vegetable growing, cattle breeding and the textile and sugar industries. The nitrate content is always linked to the type of vegetation cover. The origin of silica is mostly natural and contents vary according to the soil types crossed by rivers.

Nitrates are always more concentrated in phreatic groundwaters than surface waters. The impact of groundwaters on reef ecosystems is more important than that of surface waters.

The most damaged reefs are in areas with the highest nutrient content, the external slopes subject to plumes from Tamarin and "Trou d' Eau Douce" and in the first four meters of water in the bay of "Trou d' Eau Douce", which have elevated nutrient contents.

The decline of the reef communities of Mauritius results from a general desequilibrium due to anthropogenic activities, to the large amount of island pollutants and overfishing in the lagoons.

1. INTRODUCTION

L' île Maurice est une petite île volcanique de l' océan Indien (1840 km^2). Elle est ceinturée par un récif corallien sur 150 km de côte.

Les développements de l' agriculture depuis 1945 (culture de canne à sucre), de l' industrie (textile et sucrière) et du tourisme ont accompagnés une forte démographie et se sont effectués au détriment de l' environnement. Les pollutions sont multiples et en l' absence de traitement des eaux usées, les cours d' eau, les nappes souterraines et les lagons ont été contaminés et les réseaux trophiques déséquilibrés.

Des signes de dégradation des coraux ont été observés en 1987 (MULLER & VASSEUR, 1989), ce qui fut à la base d' un projet d' étude organisé par la Commission des Communautés Européennes (projets 946/1988, 946/1989) puis repris par le Fonds National Suisse de la Recherche (projet 21.26147.89). Mettant en collaboration plusieurs laboratoires universitaires et centres de recherche européens, suisses et mauriciens, cette étude multidisciplinaire (biologie marine, océanographie, chimie, géochimie et géologie) a permis de déterminer l' origine de ces dégradations et de mettre en évidence les impacts anthropiques sur les écosystèmes récifaux de l' île Maurice. Les résultats détaillés sont publiés dans plusieurs rapports destinés à la Direction du Développement de la CEE et du Gouvernement Mauricien ainsi que dans une thèse de doctorat (MULLER *et al.* 1991b; RUCH & MULLER 1992; GENDRE 1992).

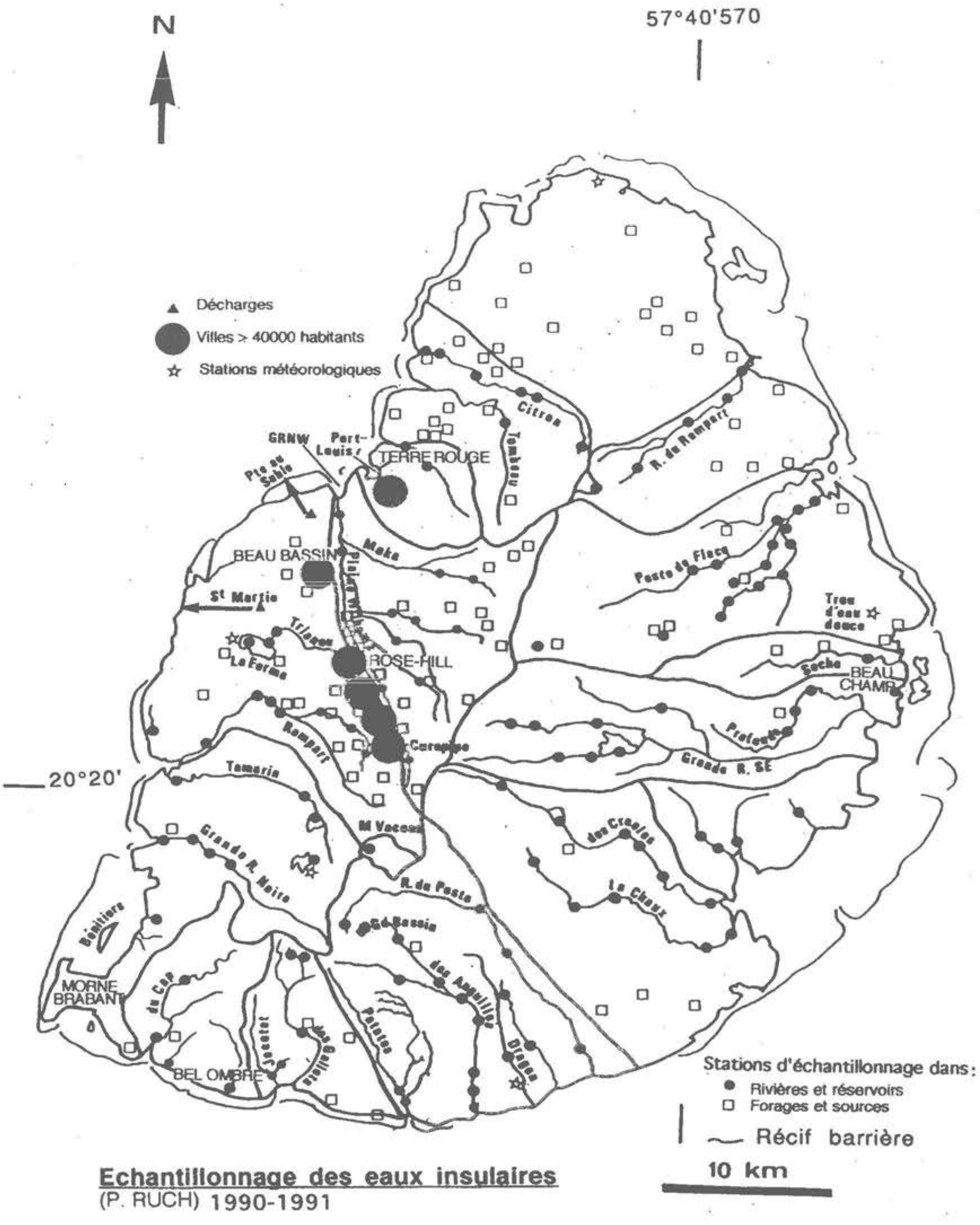

Fig. 1. Sample locations of the island water (RUCH, 1990-1991).
Fig. 1. Localisation des échantillons d'eau insulaire (RUCH, 1990-1991).

Il est largement reconnu que le développement des communautés coralliennes est soumis à plusieurs facteurs : température, salinité, turbidité, teneurs en éléments nutritifs, oxygène dissous et radiations solaires (U.V.). De nombreuses études ont montré que la variabilité de ces paramètres contrôle directement ou indirectement l' intégrité des peuplements coralliens. Des épisodes de blanchissement du corail, dus à l' expulsion massive des zooxanthelles (algues unicellulaires photosynthétiques symbiontes des coraux), ont été mis en relation avec des changements de salinité, d' oxygène dissous et de turbidité affectant les eaux de l' Atlantique (GOREAU 1964). Le même réchauffement des eaux océaniques de surface lié aux phases ENSO (El Niño Southern Oscillation) a provoqué le blanchissement des coraux dans le Pacifique (GLYNN 1984). D' autres facteurs associés à l' effet thermique, à l' augmentation du CO_2 atmosphérique (HOLLAND, LAZAR & McCAFFREY 1986) et aux radiations U.V. (ROUGERIE *et al.* 1992) peuvent aussi être impliqués dans les processus de dégradation des récifs. Un excès de nitrates et de phosphates (eutrophisation) entraîne inévitablement une prolifération des algues, ce qui peut causer la suppression de plus de 50 % de la calcification des récifs (KINSEY & DAVIES, 1979; WALKER & ORMOND 1982).

Pour cerner les causes de dégradation des récifs coralliens de l' île Maurice, nous avons donc mesuré les éléments nutritifs (nitrates, silice et phosphates) dans les eaux des lagons et des résurgences d' eau souterraine, dans les eaux océaniques avoisinantes et dans les eaux douces du réseau hydrographique. Tout ceci pour déterminer l' origine de ces éléments nutritifs.

2. ÉCHANTILLONNAGE ET MÉTHODES

Les études sur le terrain ont été réalisées suivant un rythme saisonnier entre mars 1989 et mars 1991. Deux campagnes ont été effectuées sur la côte Sud-Ouest (Rivière Noire) l' une en mars-avril (saison cyclonique) et l' autre en novembre 1989 (saison sèche); deux autres campagnes ont eu lieu sur la côte Est (Trou d' Eau Douce) en avril et novembre 1990. Ces sites ont été choisis car ils diffèrent par leurs potentiels économiques (agriculture, industrie), par leur impact démographique, par leur exposition aux vents et par leur réseau hydrographique (de surface et souterrain).

Les analyses des échantillons d' eau prélevés durant les quatre campagnes de terrain ont été réalisées par FIA (Flow Injection Analysis) par le laboratoire de géochimie de l' Université de Neuchâtel. De plus, un contrôle des eaux insulaires et lagonaires (Fig. 1) a été rendu possible par l' installation d' une antenne de suivi d' avril 90 à mars 91.

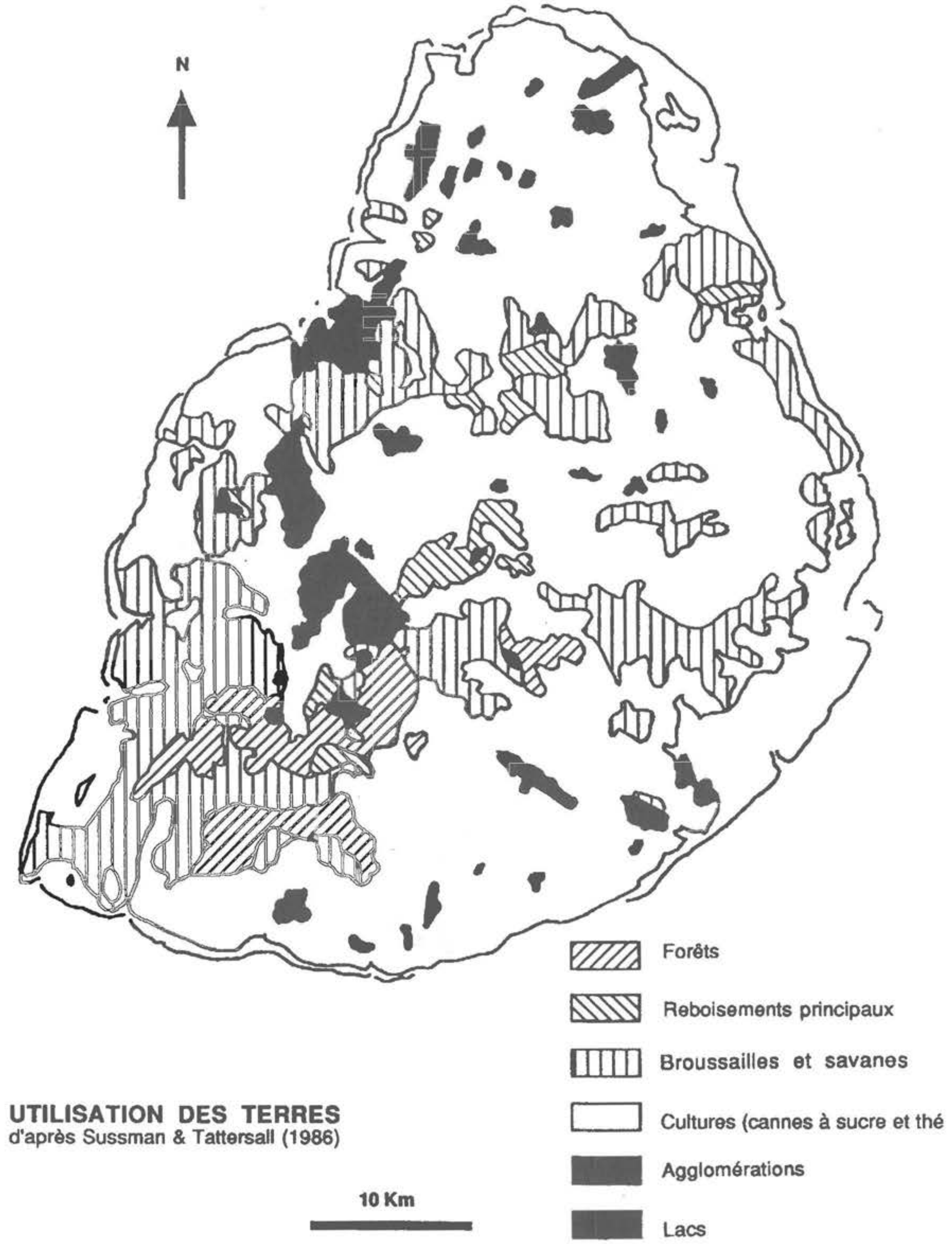

Fig. 2. Utilisation of lands (SUSSMAN & TATTERSALL, 1986).
Fig. 2. Utilisation des terres (SUSSMAN & TATTERSALL, 1986).

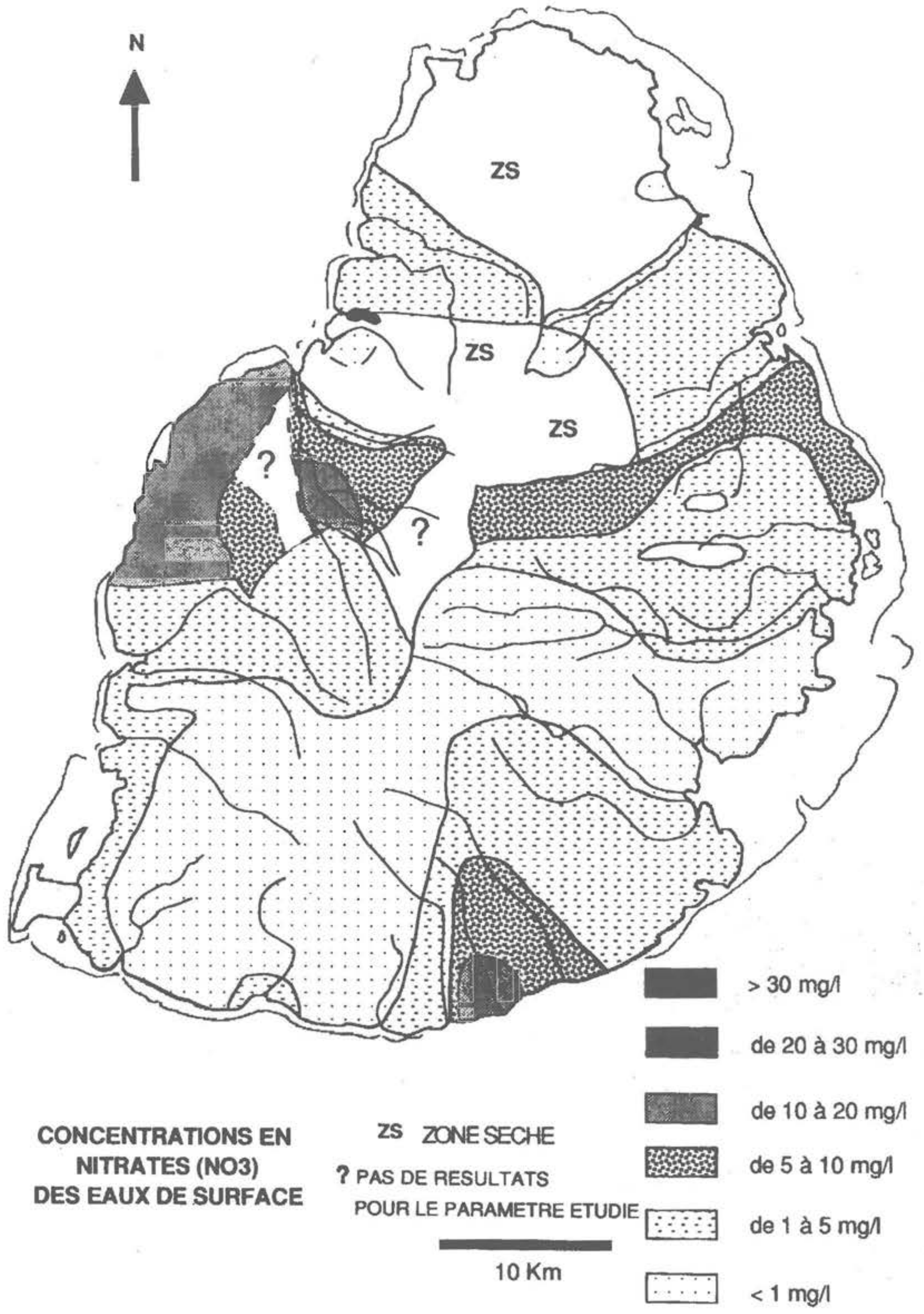

Fig. 3. Concentrations in nitrates (NO3) in superficial waters.
Fig. 3. Concentrations en nitrates (NO3) dans les eaux de surface.

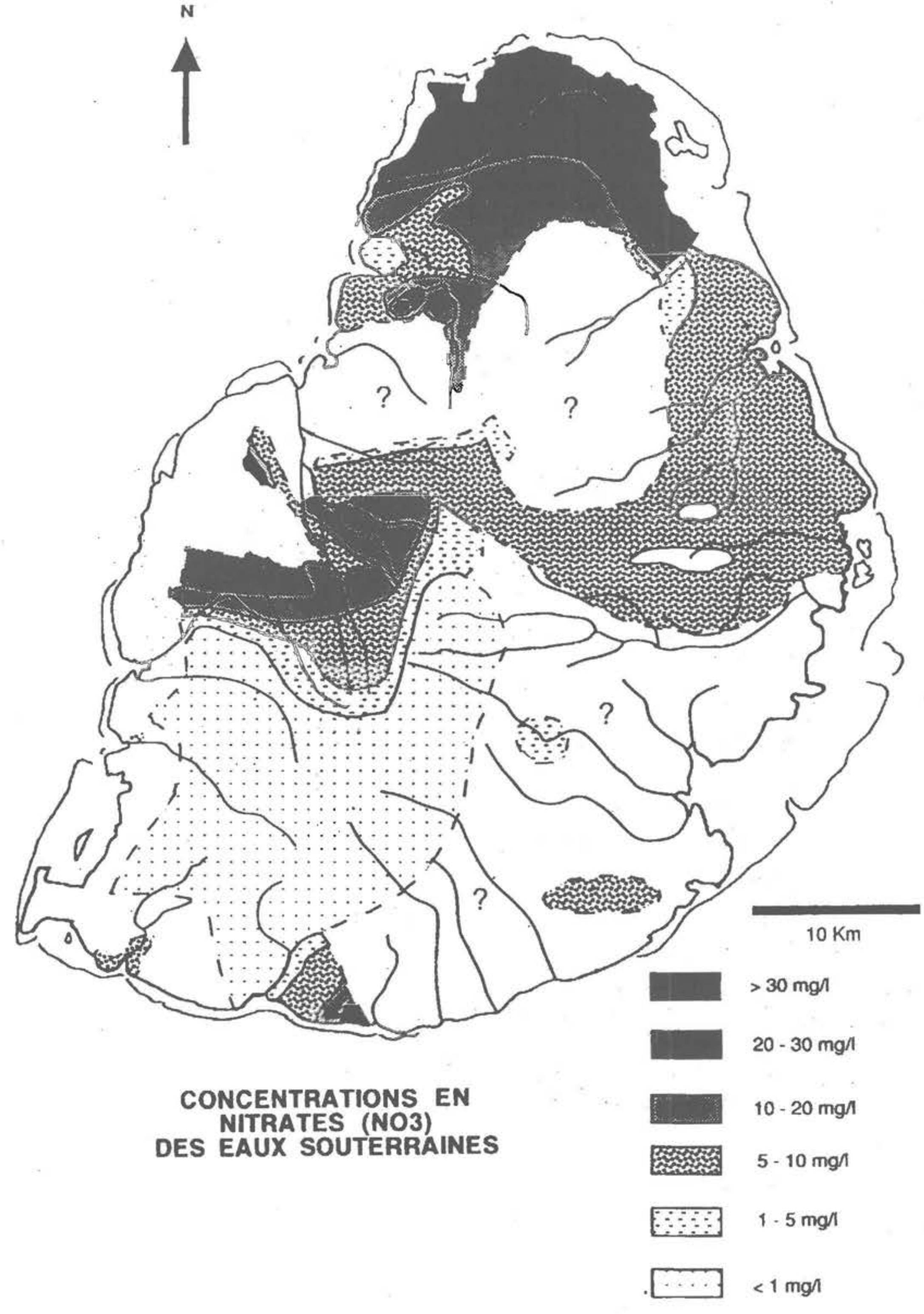

Fig. 4. Concentrations in nitrates (NO3) in underground waters.
Fig. 4. Concentrations en nitrates (NO3) dans les eaux souterraines.

La méthode FIA "Flow Injection Analysis" de la firme Tecator permet l' analyse d' un paramètre donné (NO_3, SiO_2 ou PO_4) sur 40 échantillons en série. Le principe est un dosage colorimétrique selon une méthodologie développée par RUZICKA & HANSEN (1981).

3. RÉSULTATS ET DISCUSSION

3.1. Teneurs en éléments nutritifs des eaux douces (fractions dissoutes inorganiques)

Les teneurs en silice des eaux du réseau hydrographique de surface sont liées à la nature des sols lessivés et traversés par les rivières puisque les valeurs mesurées s' élèvent d' amont en aval. En amont de la Grande Rivière Noire (sur le Plateau Central), on mesure 1 mg/l de silice (fraction réactive inorganique dissoute). Au passage sur des laves basaltiques riches en silice, les eaux s' enrichissent et se jettent dans les lagons du Sud-Ouest avec des teneurs de l' ordre de 25 mg/l. A l' île Maurice, la silice n' est donc pas un marqueur typiquement anthropique.

Des sources importantes de phosphates sont liées aux engrais des cultures maraîchères, aux élevages, aux industries textiles et sucrières. Durant le broyage, la canne à sucre restitue jusqu' à 50 mg/l de phosphates et un peu de silice. Ces phosphates peuvent être rapidement consommés par le phytoplancton et les algues benthiques; leurs teneurs montrent une très grande variabilité suivant le débit des cours d' eau.

Les teneurs en nitrates des eaux douces insulaires apparaissent liées à la nature du couvert végétal (Fig. 2, 3 et 4). Sur le Plateau Central couvert de forêts primaires, les teneurs dans les eaux de surface et souterraines sont les plus basses mesurées sur l' île (< 5 mg/l). Par contre, dans les régions agricoles (cannes à sucre, zone Est), les concentrations atteignent 10 mg/l. A l' Ouest, la présence de nitrates dans les eaux insulaires est également liée aux cultures et élevages et en plus faible part à l' urbanisation.
Les nitrates sont toujours plus abondants dans les nappes phréatiques que dans les

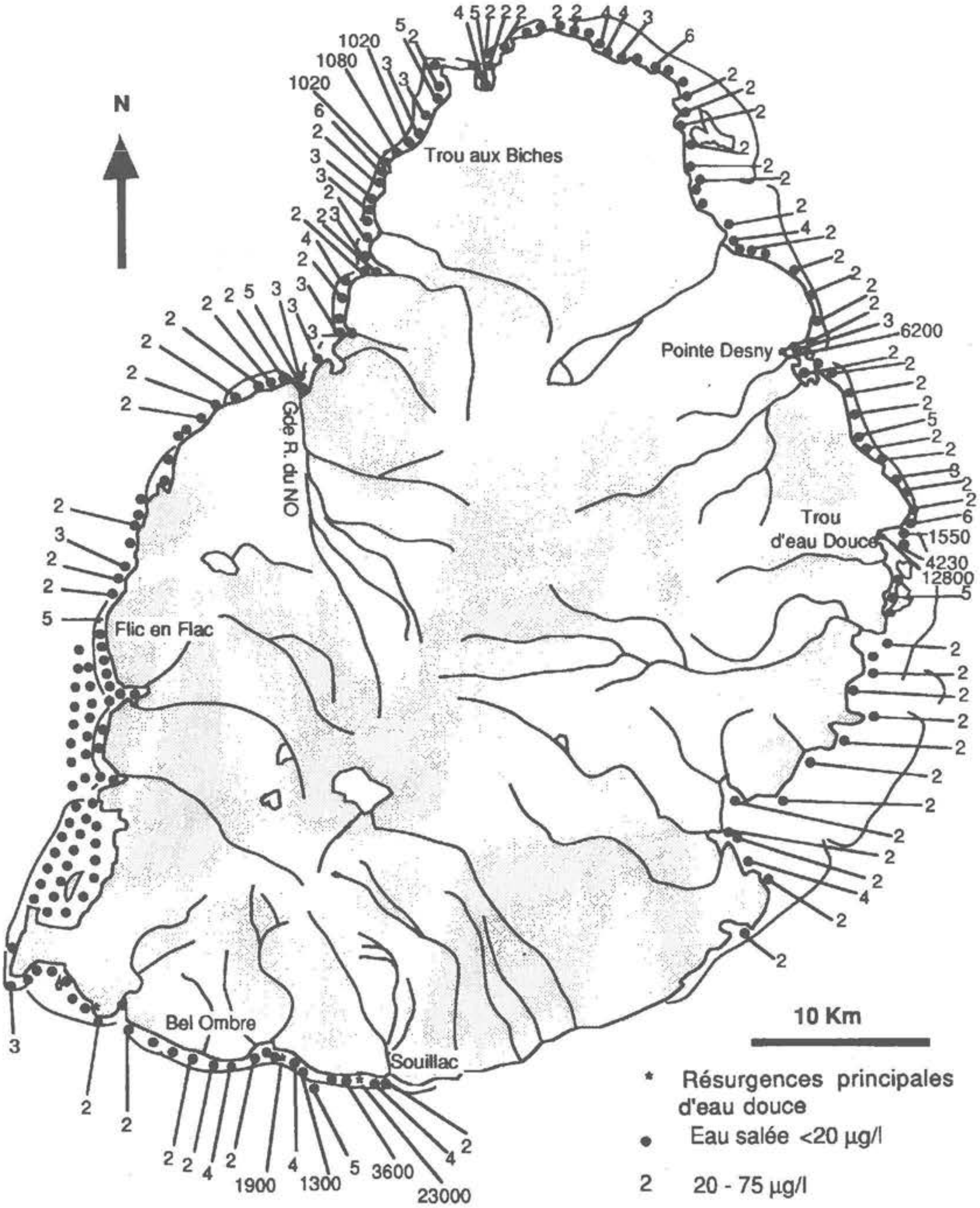

Fig. 5. The nitrates content (NO3) in lagoons.
Fig. 5. Les teneurs en nitrates (NO3) dans les lagons.

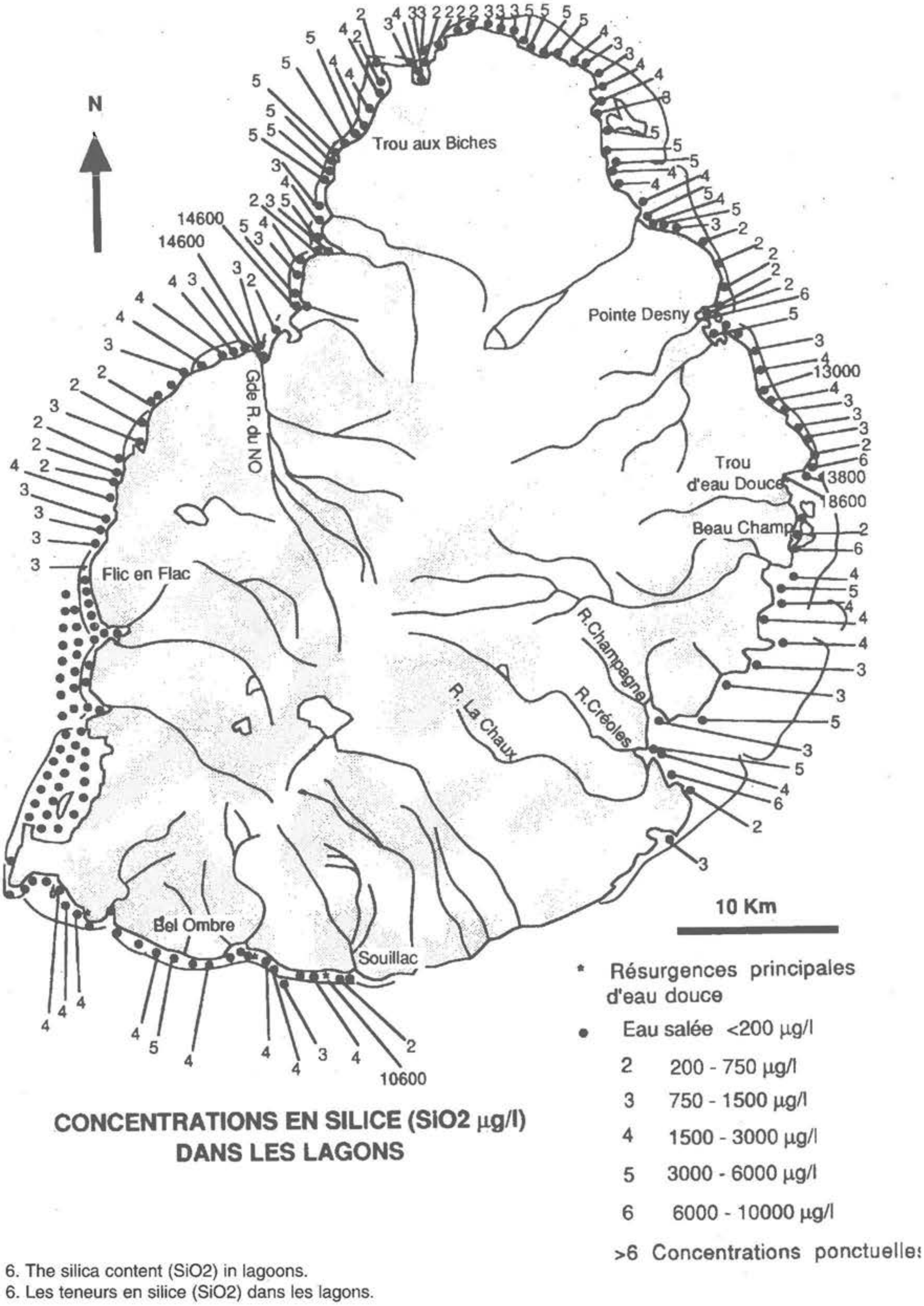

Fig. 6. The silica content (SiO2) in lagoons.
Fig. 6. Les teneurs en silice (SiO2) dans les lagons.

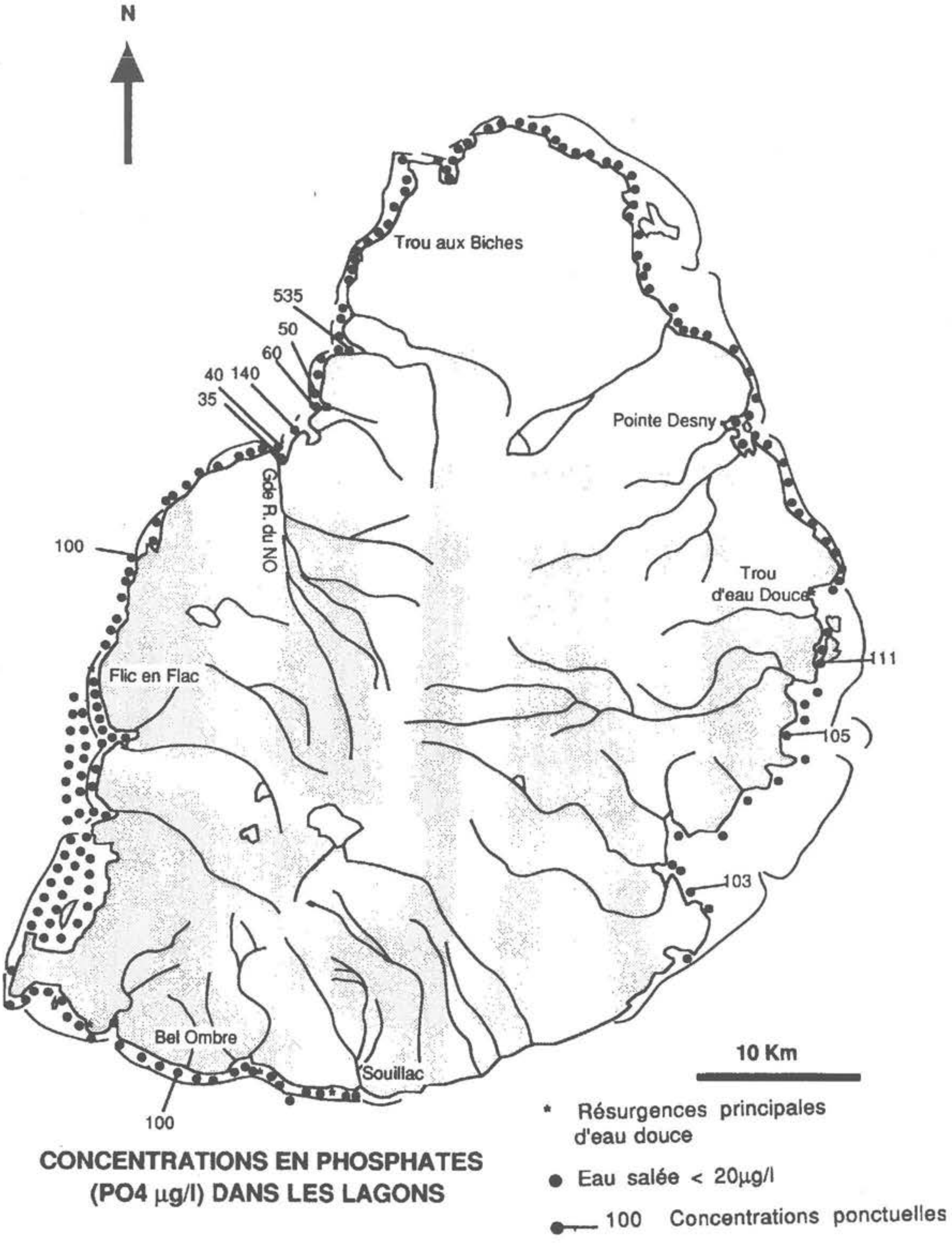

Fig. 7. The phospates content (PO4) in lagoons.
Fig. 7. Les teneurs en phosphates (PO4) dans les lagons.

eaux de surface, de plus on mesure des teneurs en nitrates élevées dans des régions souterraines beaucoup plus étendues qu' en surface, comme par exemple à l' Est (Fig. 3 et 4).

Les concentrations en nitrates dans les rivières et réservoirs sont variables en fonction de la pluviosité et du lessivage des champs; au contraire, les teneurs restent à peu près constantes dans les nappes phréatiques où l' activité biologique est limitée. Les apports en nitrates dans les lagons soumis à l' influence de résurgences d' eau souterraine, sont donc importants toute l' année. Dans la baie de Trou d' Eau Douce, où les apports en eau douce se font exclusivement par des résurgences, les teneurs en éléments nutritifs sont élevées, quelle que soit la pluviométrie ($NO_3 \approx 10$ mg/l, $SiO_2 \approx 20$ mg/l, $PO_4 \approx 100$ µg/l).

Etant plus riches en éléments nutritifs, les eaux souterraines ont alors un impact plus important sur l' écosystème récifal que celui des eaux de surface, dont les teneurs sont plus fluctuantes.

3.2. **Teneurs en éléments nutritifs des eaux marines** (fractions dissoutes inorganiques)

L' océan Indien tropical est oligotrophe du fait que les éléments nutritifs qui sont présents à partir de 100-200 m de profondeur (eaux intermédiaires) ne peuvent remonter en surface par phénomène d' upwelling : la stratification thermique entretient un découplage entre le système superficiel chaud et les systèmes intermédiaire et profond riches en éléments nutritifs. On rappelle que le maintien d' eaux oligotrophes et claires est une condition "sine qua non" à la pérennité des récifs et atolls coralliens et que ceux-ci sont absents des zones enrichies en éléments nutritifs, eutrophisées ou polluées (HALLOCK & SCHLAGER 1986).

Les éléments nutritifs mesurés au large de l' écosystème récifal donnent des réactions très basses, les teneurs lagonaires sont beaucoup plus élevées et résultent de l' utilisation des terres sur les bassins versants, de la pluviométrie et du système d' écoulement des eaux (phréatique et de surface).

Les régions littorales et lagonaires soumises à l' influence de bassins versants encore couverts par la végétation primaire, comme le Sud-Ouest de l' île, ont les concentrations en éléments nutritifs les plus basses : $NO_3 < 30$ µg/l, $PO_4 < 30$ µg/l, $SiO_2 \approx 200$ µg/l (Fig. 5, 6 et 7). Les teneurs mesurées sont variables selon la saison, avec des maxima dans les baies en période cyclonique : $NO_3 = 300$ µg/l, $PO_4 < 30$ µg/l, $SiO_2 \approx 3$ à 10 mg/l.

Tous les lagons ayant des teneurs en éléments nutritifs élevées se situent en aval des zones à forte emprise anthropique.

Des teneurs en nitrates de 0.3 à 23 mg/l, ont été mesurées dans le Sud, à l' Est et au Nord-Ouest. Les teneurs en nitrates supérieures à 1 mg/l et pouvant atteindre ponctuellement 23 mg/l, ont toujours été mesurées près des résurgences d' eau souterraine connues ou visibles à l' œil nu (Fig. 5). L' impact des eaux des nappes phréatiques sur les eaux lagonaires est donc supérieur à celui des eaux du réseau de surface. Les résurgences d' eau douce jouent ainsi un rôle prépondérant dans la qualité des eaux littorales et lagonaires.

Les maxima de concentration en silice (3 à 18 mg/l) coïncident avec les concentrations en nitrates les plus élevées et se situent donc près des résurgences d' eau douce (Fig. 6). Les teneurs en silice sont également fortes dans les estuaires des grandes rivières et aux abords des usines sucrières de Bel Ombre et Beau Champ.

Les concentrations en phosphates (Fig. 7) sont généralement faibles dans les eaux des lagons (PO_4 < 20 µg/l). Quelques teneurs plus élevées (max : 535 µg/l) sont liées à la proximité d' agglomérations et d' industries, dans la région de Port-Louis et des usines sucrières de Bel Ombre et Beau Champ.

3.3. État de santé des écosystèmes coralliens

Autour de l' île Maurice, l' état des écosystèmes littoraux est préoccupant du fait du développement de certaines maladies coralliennes (ANTONIUS 1991, *in* : MULLER *et al.* 1991), de la prolifération des algues et des oursins : la communauté corallienne est donc en forte régression.

Les apports insulaires d' éléments nutritifs identifiés dans cette étude, causent un déséquilibre du milieu littoral et lagonaire. Il est connu que les coraux sont fragilisés dans une situation de type eutrophique et deviennent plus sensibles aux attaques bactériennes (MITCHELL & CHET 1975) et autres maladies (ANTONIUS 1981). Certaines d' entre elles ont une origine bactérienne et sont contagieuses comme la "Black Band Disease" où des cyanobactéries attaquent le corail et dissolvent les tissus vivants en utilisant leurs produits de décomposition comme nutriments. Dans le cas de la "White Band Disease", agression toxique causée par des cyanobactéries, le squelette calcaire est découvert de quelques mm par 24 h. D' autres maladies sont des réactions de stress de polypes coralliens en milieu déséquilibré comme la "Shut Down reaction", très contagieuse et qui désintègre les tissus à une vitesse de 10 cm/h, rappelons aussi le blanchissement du corail qui se traduit par l' expulsion des zooxanthelles, l' arrêt de la calcification et une mortalité significative. Une maladie spécifique aux coraux de l' île Maurice (ANTONIUS, observation 1991), est probablement due à des germes pathogènes et affecte les coraux survivants près des émissaires des industries sucrières. Ces différents types de maladies, causées directement ou indirectement par des cyanobactéries sont donc de bons marqueurs de pollution et d' eutrophisation de l' environnement récifo-lagonaire.

Ordinairement, les algues et les coraux vivent en harmonie et équilibre. Cependant, sur les pentes externes de la barrière de la côte Est, des algues gazonnantes envahissent l' écosystème récifal et atteignent jusqu' à 60 à 100 % de recouvrement (BALLESTEROS, 1991 *in* MULLER *et al.* 1991b). Le développement d' algues thionitrophiles (*Ulva pulchra, Ulva reticulata*) face à l' estuaire de la Grande Rivière du Sud-Est indique un milieu riche en nitrates et une eutrophisation importante.

La pêche intensive, qui induit la pêche des spécimens immatures, a largement contribué à la décroissance de la population piscicole. Les populations des poissons herbivores, des poissons producteurs de sable (perroquets, balistes) et des prédateurs sont fortement réduites par rapport à ce qu' elles sont dans d' autres environnements récifaux (observations Nouméa, Nouvelle Calédonie : KÜBLER 1991 et Sharm-el-Sheikh, Egypte : KÜBLER *et al.* 1994).

Favorisés par la couverture d' algues et la disparition de leurs prédateurs (balistes, raies etc...), les oursins prolifèrent de façon importante et modifient la qualité du biotope. L' action bioérosive d' *Echinometra mathaei* sur les carbonates est bien connue (BIRKELAND 1969) et équivaut à une érosion de la barrière récifale de 4 à 12 mm par an (MEYER *et al.* 1991, *in* MULLER *et al.* 1991b). La conséquence majeure de la colonisation du récif par les oursins est donc une fragilisation de la barrière et une limitation de la croissance des coraux.

La comparaison de la faune benthique actuelle (HOTTINGER 1991 *in* MULLER *et al.,* 1991) au recensement effectué 10 ans auparavant (MONTAGGIONI 1981) montre que les grands foraminifères ont presque disparu en faveur des plus petits et qu' ils sont quasiment absents en deçà de l' isobathe 10 mètres. De plus, la microradiographie révèle la présence fréquente de défauts de calcification et de malformations des loges chez les grands foraminifères (PÉCHEUX, *in* MULLER *et al.* 1989). Certains foraminifères (*Anomalinella rostrata* et *Eponides repandus*) présents dans les premiers 25 m d' eau, sont de précieux indicateurs d' eutrophisation de la colonne d' eau. Dans l' océan et par grande profondeur (> 200 m), la répartition et le nombre des foraminifères deviennent à nouveau comparables à ceux rencontrés en Mer Rouge, ce qui confirme le déséquilibre faunistique des eaux lagonaires autour de l' île Maurice.

La comparaison des photographies aériennes des zones sud-ouest et est, prises en 1974 et en 1989-90, montre la régression générale des herbiers à Phanérogames (frayères et abris pour les poissons juvéniles), l' érosion des plages et la redistribution du sable et surtout la disparition de larges champs de colonies coralliennes.
Une comparaison avec nos cartes de distribution des éléments nutritifs montre que les récifs les plus dégradés se rencontrent dans les zones riches en éléments nutritifs et/ou très turbides. La dégradation des récifs frangeants et lagonaires est surtout

marquée dans les premiers 10 mètres d' eau où s' effectue le mélange entre les eaux douces et marines. Par exemple, les récifs frangeants de Tamarin et de La Preneuse sont sous l' influence du panache saumâtre issu de l' estuaire de Tamarin et sont les plus dégradés de la côte sud-ouest.

A l' Est, l' eutrophisation et la prolifération d' algues atteignent la pente externe du récif barrière, soumise à l' influence du panache issu de la baie de Trou d' Eau Douce. Dans cette baie de Trou d' Eau Douce, les coraux sont fortement dégradés au niveau des trois à quatre premiers mètres (eau plus douce et fortement concentrée en éléments nutritifs), ce qui montre bien la relation entre dégradation corallienne et présence d' eau douce riche en éléments nutritifs.

Dans les lagons du Sud-Ouest, où les apports en eaux douces le sont en majorité par des rivières, les teneurs en éléments nutritifs varient avec la pluviosité. On a noté dans ce cas que la croissance des coraux suit un rythme saisonnier : les coraux ont repris une certaine vitalité après la saison cyclonique de 1989; des massifs d' Acropores branchus du lagon de La Preneuse nécrosés à la base, ont repoussé à partir de l' extrémité des branches pendant la période sèche de 1990-91 (particulièrement longue et ayant limité les apports dans les lagons; RUCH & GENDRE, observation 1991).

4. CONCLUSION

La dégradation des coraux autour de l' île Maurice résulte d' un déséquilibre général du milieu récifo-lagonaire causé essentiellement par les activités anthropiques. Ce déséquilibre est dû aux apports insulaires par lessivage des sols (sels nutritifs, pesticides, eaux usées domestiques et industrielles). Les dégradations résultant de ces déséquilibres et excès en éléments nutritifs sont de type eutrophique et apparaissent dans les niveaux superficiels. L' apport en eau douce n' est cependant pas le facteur essentiel de la dégradation actuelle puisque les coraux, jadis florissants étaient évidemment soumis à son influence. Les fortes teneurs en phosphates et surtout en nitrates sont indirectement responsables de la mort des coraux, du fait de la prolifération des algues, de l' apparition des bioérosions et des maladies d' origine bactérienne.

La pêche intensive, par élimination des poissons brouteurs et nettoyeurs, a dépeuplé les lagons et contribué à augmenter le déséquilibre du milieu. Le développement des algues, engendré par les excédents en sels nutritifs tend à empêcher la croissance normale des coraux. La prolifération des oursins est également facilitée par le développement des algues et par la disparition de leurs prédateurs, victimes de la pêche intensive. Ces oursins aggravent l' érosion de la barrière de corail et participent activement à la fragilisation et à la régression du récif.

Les coraux soumis à ces multiples stress résistent moins aux maladies (attaques bactériennes) et aux événements catastrophiques comme les cyclones. Des pans entiers de récifs se dégradent et meurent, engendrant des modifications de l' hydrodynamisme lagonaire et une érosion accrue des plages. L' écosystème récifo-lagonaire de l' île Maurice est donc entré dans une phase de dégradation intense, comme le sont malheureusement la plupart de ses homologues insulaires (GUILCHER 1988).

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IMPACTS ANTHROPIQUES SUR LES ÉCOSYSTÈMES RÉCIFAUX ET CÔTIERS DE L' ÎLE MAURICE (SW OCÉAN INDIEN) : LE COPROSTANOL DANS LES SÉDIMENTS DE SURFACE, INDICATEUR DES EAUX USÉES.

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Résumé - Le coprostanol est un remarquable marqueur de pollution fécale. Nous l' avons dosé sur 63 échantillons de sédiments marins prélevés dans les lagons autour de l' île Maurice.

86% des échantillons ont des teneurs en coprostanol supérieures à 0,2 mg/kg. Quasiment tous les sites étudiés sont contaminés, exceptée la baie de Tamarin (côte Sud-Ouest) qui est brassée par les fortes houles océaniques.

L' estuaire de la Grande Rivière Nord-Ouest à Port-Louis (capitale de l' île, côte Ouest), celui de la Grande Rivière du Sud-Est, la région de l' hôtel Touessrok et la sortie du chenal de Trou d' Eau Douce (côte Est) sont les sites les plus contaminés par les eaux usées, avec des teneurs en coprostanol supérieures à 1,5 mg/kg.

L' impact des eaux usées diminue avec l' éloignement de la côte et la profondeur, mais il persiste toujours 0,9 mg/kg par 190 m de profondeur (côte Sud-Ouest).

Abstract - Coprostanol, a reliable marker of fecal pollution, has been determined from 63 marine sediment samples taken in lagoons around Mauritius island.

86% of sediment samples contained more than 0.2 mg/kg of coprostanol, indicating a significant fecal pollution. Contamination was detected at all the sites studied, except in ' Tamarin' bay (South-West coast) which is strongly wave beaten.

'Grande Rivière Nord-Ouest' estuary in Port-Louis (capital, West coast), ' Grande Rivière du Sud-Est' estuary, area near Touessrok hotel and the opening of the ' Trou d' Eau Douce' channel (East coast) were the sites most contaminated by sewage pollution, with coprostanol contents higher than 1,5 mg/kg.

Sewage impact decreases with distance from the coast and depth. Lower coprostanol concentrations were generally encounted in the open sea sediments, but at 190 m depth (South-West coast) the coprostanol concentration was always relatively high (0,9 mg/kg).

1. INTRODUCTION

L' île Maurice se situe dans la partie australe de l' océan Indien par 20° de latitude Sud et 57° de longitude Est. Elle constitue, avec La Réunion et Rodrigues, l' archipel des Mascareignes situé à 800 km à l' Est de Madagascar et à 2000 km de la côte africaine.

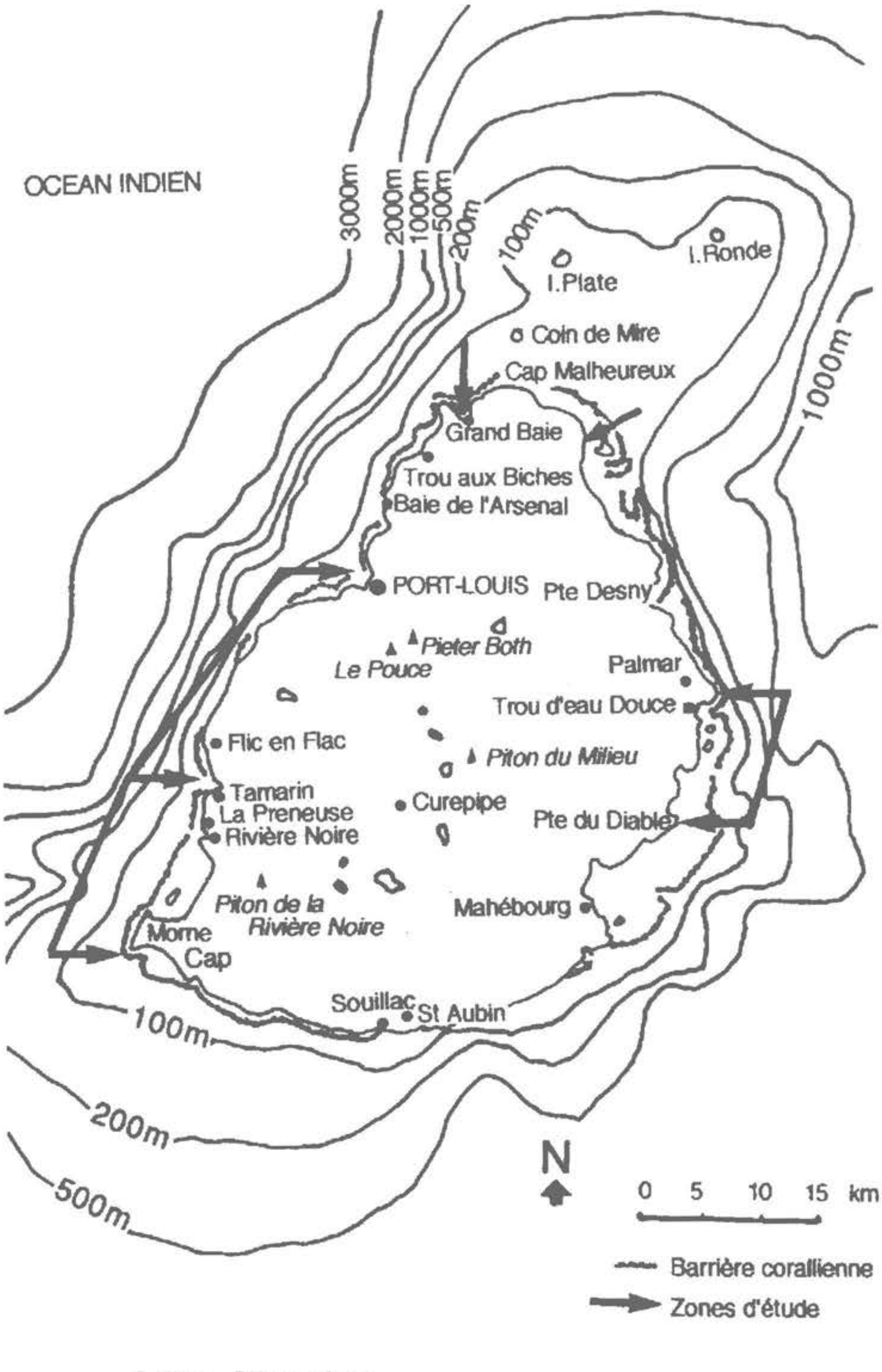

Fig. 1. Sample locations
Fig. 1. Localisation des campagnes d'échantillonnage.

L' île a une superficie de 1840 km^2 et est entourée d' un plateau immergé qui peut s' étendre jusqu' à 25 km de la côte. Une ceinture de récifs coralliens s' est développée à une distance du littoral allant de quelques centaines de mètres à 5 km et ce presque tout autour de l' île sur 150 km (BATTISTINI 1970).

A l' heure actuelle, l' île est peuplée de plus d' un million d' habitants originaires d' Europe, d' Asie et d' Afrique. Durant les cinquante dernières années, l' île s' est fortement développée dans les secteurs urbain, industriel, agricole et touristique au détriment de l' environnement. Cela a entraîné des pollutions anthropiques, la surexploitation des lagons et l' extension des travaux d' aménagement du littoral qui ont causé de façon indirecte ou directe des dégradations des écosystèmes coralliens (JOHANNES 1975).

On sait que les systèmes d' assainissement des eaux usées sont insuffisants (MULLER *et al.* 1991b; RUCH & MULLER 1992), les eaux urbaines et les effluents industriels ne sont pas traités et sont soit acheminés par un système d' égout vers la mer, soit directement rejetés dans les rivières et les lagons. Les plus grands hôtels sont en général équipés de stations d' épuration mais des problèmes de traitement des eaux usées existent encore. Les élevages intensifs rejettent également des déchets fécaux directement dans les lagons.

De nombreux facteurs tendent à déséquilibrer le milieu récifo-lagonaire, entraînant la dégradation des récifs coralliens. Diverses sources de pollution (agriculture, industries, élevages) et leurs impacts ayant déjà été étudié (GENDRE 1992), nous nous limiterons à présenter ici, l' impact anthropique évalué à partir d' un facteur de pollution fécale.

Le dosage du coprostanol (5 b-cholestan-3 b-ol) est une méthode plus intéressante que le comptage des coliformes pour évaluer l' impact des eaux usées (PITTET 1990). Ce produit a plusieurs avantages par rapport aux mesures traditionnelles de contamination fécale : il est chimiquement stable dans l' environnement aquatique et est peu affecté par des variables physico-chimiques comme la température, le chlore, les polluants organiques etc... Le coprostanol est un traceur de pollution fécale très spécifique produit par réduction bactérienne intestinale du cholestérol (MURTAUGH & BUNCH 1967; DUTKA *et al.* 1973; YDE *et al.* 1982). C' est l' un des principaux stérols trouvés dans les fèces humains et des mammifères supérieurs (ROSENFELD & GALLAGHER 1964).

2. ÉCHANTILLONNAGE ET MÉTHODES

La quantification du coprostanol et autres paramètres de la matière organique, COA (carbone organique acidosoluble), COTC (carbone organique total calculé) a été réalisée sur 63 échantillons de sédiment de surface prélevés de 1989 à 1992 autour de l' île Maurice (Fig. 1).

Les échantillons sont prélevés avec une benne, puis séchés sur place à l' air libre. Les paramètres de la matière organique sont analysés par CHN Carlo Erba 1108 au laboratoire de géochimie de l' Institut de géologie de l' Université de Neuchâtel. Le coprostanol est extrait du sédiment en suivant la méthode recommandée par PIERCE & BROWN (1984). Elle peut être résumée ainsi :

- extraction durant 100 heures sur 60 g de sédiment sec, en utilisant un mélange azéotropique composé de méthanol/toluène 72,5/27,5 v/v.
- addition d' un standard interne (prégnénolone, qui est absent du sédiment).
- saponification avec des volumes égaux d' eau et d' hydroxyde de potassium 0,5 N dans du méthanol.
- neutralisation avec l' acide chlorhydrique 0,1 M.
- extraction en utilisant trois fois 50 ml de dichlorométhane.
- séparation par chromatographie sur colonne de verre contenant du gel de silice . Elution avec de l' hexane, du dichlorométhane et du méthanol. Conservation de la phase alcoolique (méthanol) contenant les stanols et stérols.
- évaporation du méthanol à sec sous un flux d' azote.
- les dérivés des stérols et stanols sont formés par silanisation en utilisant un volume de triméthychlorosilane, deux volumes d' hexaméthyldisilazane et un volume de pyridine (accélérateur de réaction).
- après 10 minutes, environ 1 µl de solution est injecté dans un chromatographe en phase gazeuse de marque Perkin-Elmer 8500.
- le coprostanol est déterminé à partir des aires des pics par comparaison avec une courbe étalon.

3. RÉSULTATS ET DISCUSSION

Les teneurs en coprostanol et celles des paramètres de la matière organique varient dans le même sens mais ne sont pas liées. Les corrélations basées sur 57 observations sont positives mais non significatives, ce qui indique une autre origine du coprostanol.

Il n' y a aucune corrélation entre les teneurs en coprostanol et les teneurs des paramètres de la phase détritique terrigène ni avec celles des paramètres de la phase carbonatée (autochtone dans le cas de l' île Maurice).

Les concentrations en coprostanol sont inversément proportionnelles à la taille des particules en suspension : le coprostanol est véhiculé avec les boues et sédimente dans des lieux calmes avec les particules fines (HATCHER & McGILLIVARY 1979). Une concentration en coprostanol supérieure à 0,01 mg/kg de sédiment sec suffit pour être révélatrice d' une contamination (PIERCE & BROWN 1984). Dans cette étude, notre seuil de quantification en mg/kg de sédiment sec est de 0,2 et l' erreur de mesure se situe autour de 20 %.

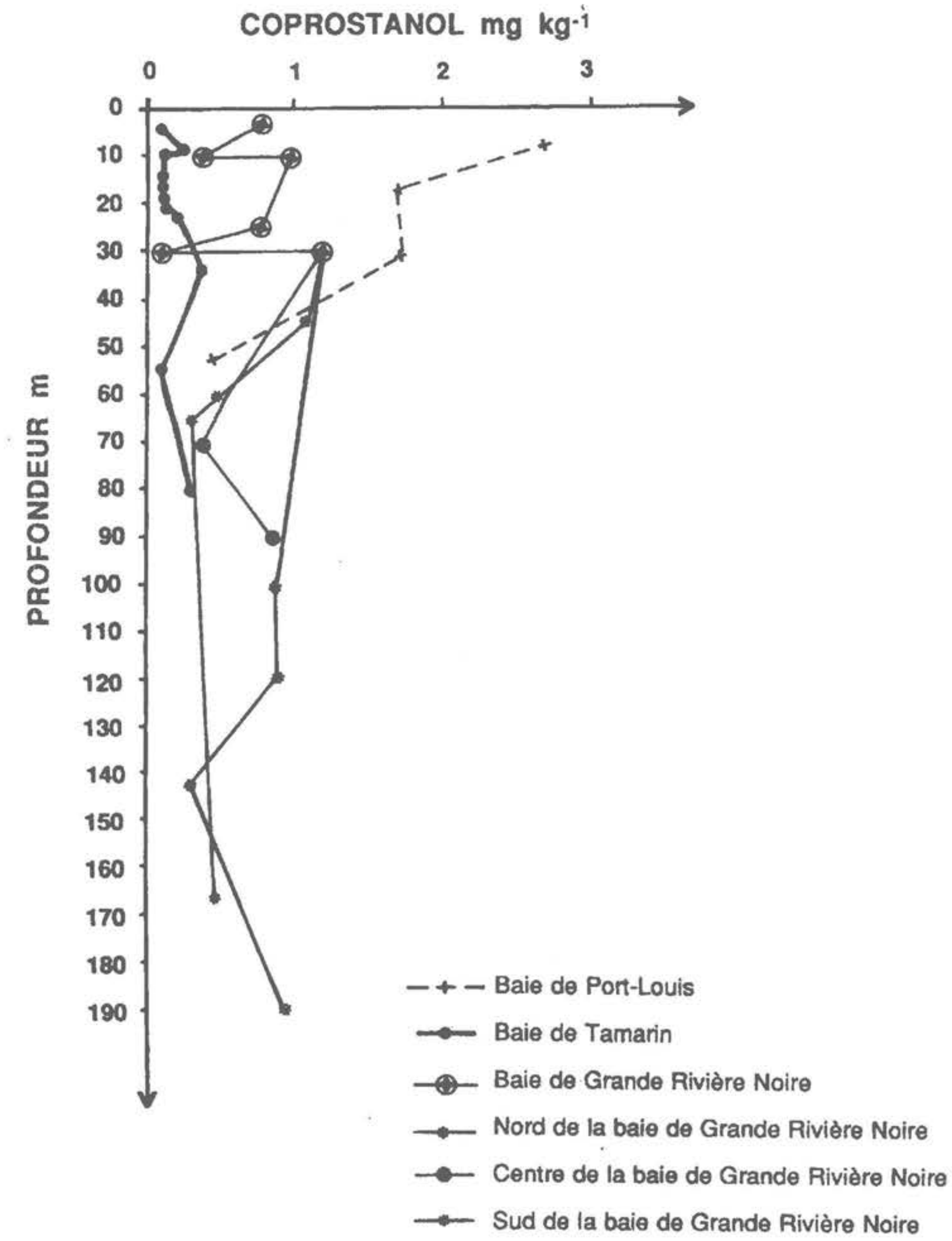

Fig. 2. Coprostanol rates in surface sediments as a function of water depth.
Fig. 2. Teneurs en coprostanol dans les sédiments de surface en fonction de la profondeur d'eau.

En guise de référence, le coprostanol a été dosé dans des sédiments de surface prélevés en Atlantique par 4800 m de profondeur; les teneurs y sont inférieures à 0,2 mg/kg. Par contre, HATCHER & McGILLIVARY (1979) mesurent 5800 mg/kg de coprostanol dans les sédiments très pollués de la baie de New York. PITTET (1990) mesure dans le lac de Neuchâtel, 50 mg/kg de coprostanol à 40 m de l' exutoire de la station d' épuration et 1,6 mg/kg dans les sédiments de surface prélevés au milieu du lac.

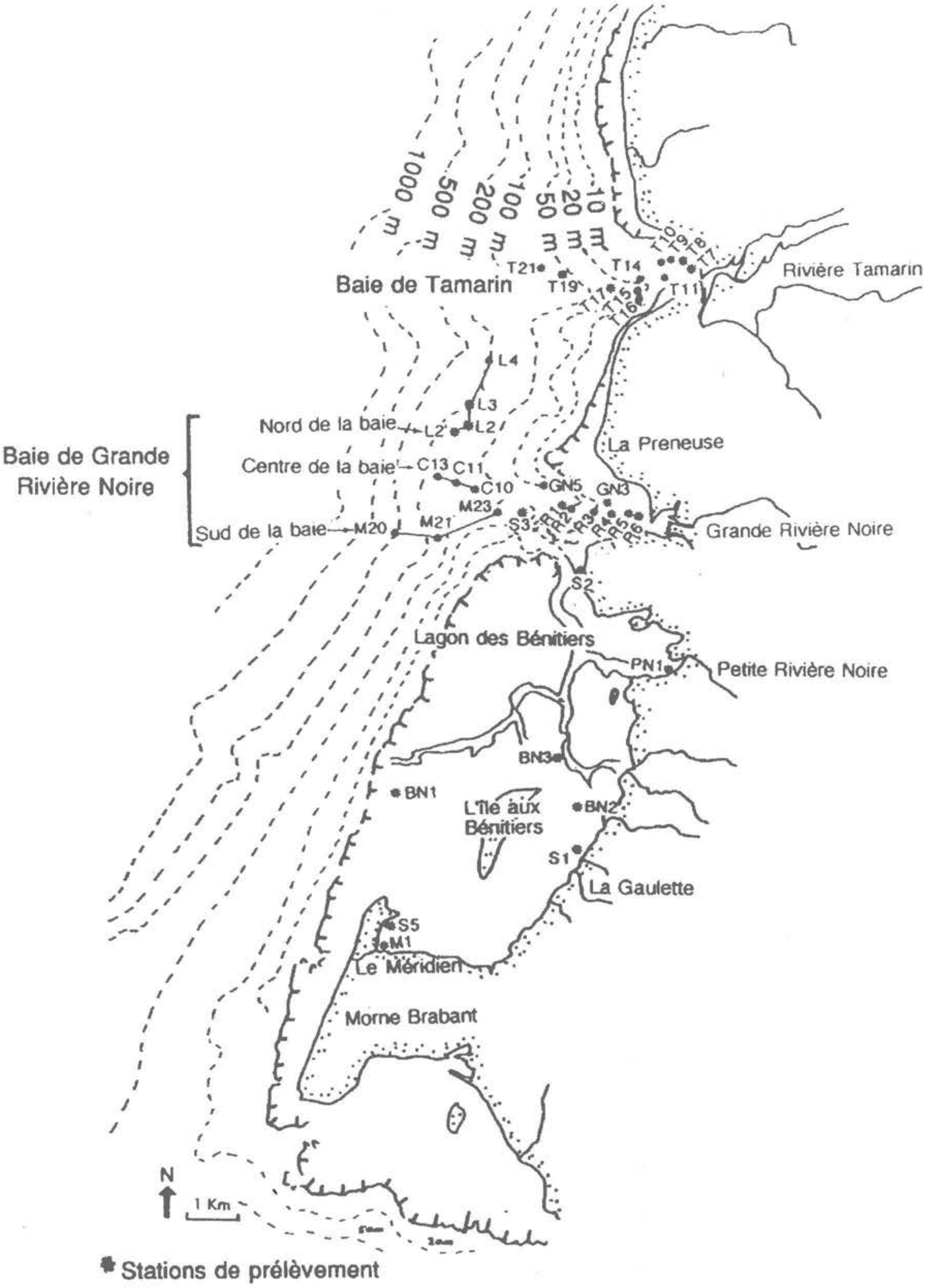

Fig. 3. Sample locations between the 'Morne Brabant' and 'Flic-en-Flac' (west coast).
Fig. 3. Localisation des échantillons entre le Morne Brabant et Flic-en-Flac (côte ouest).

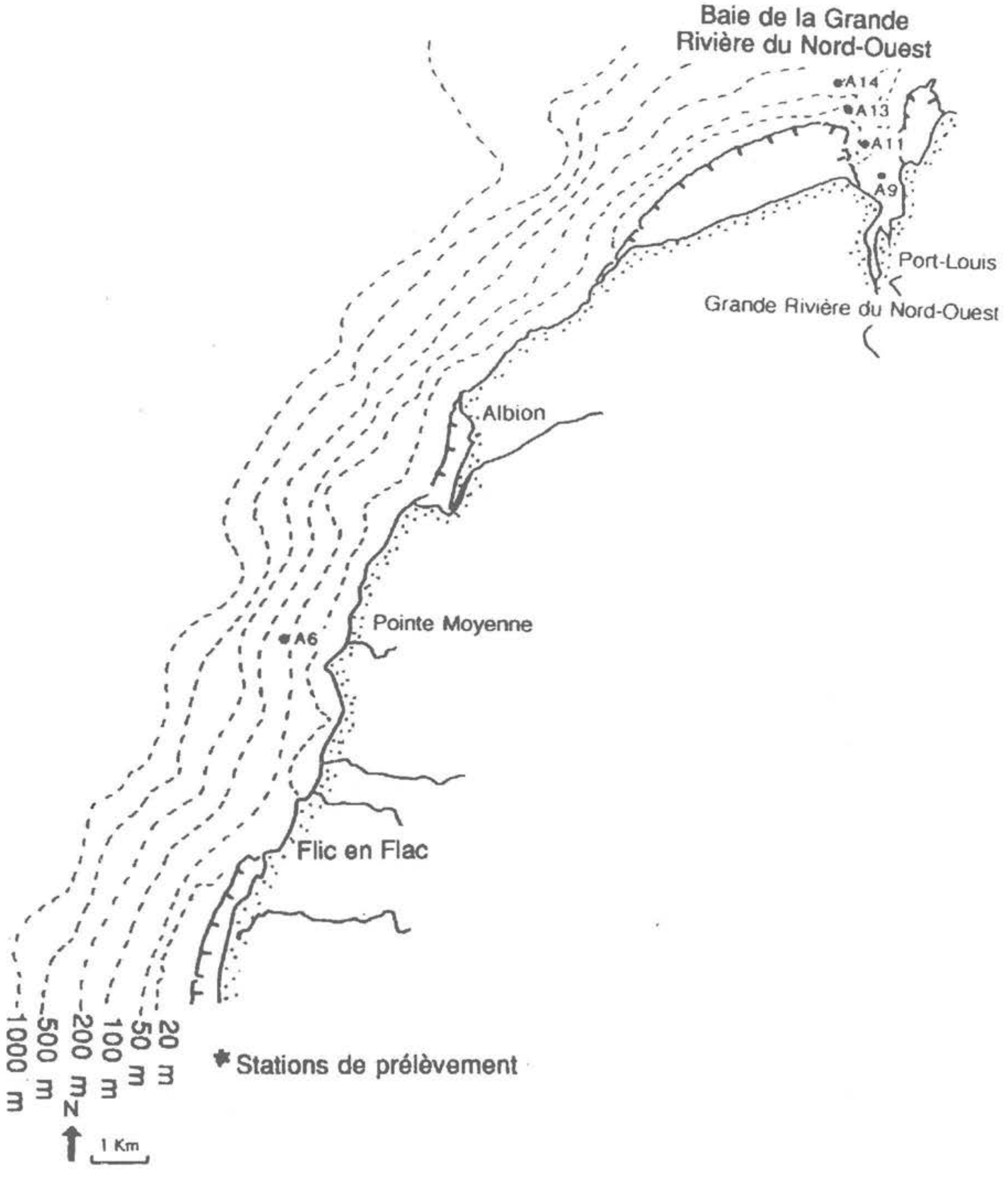

Fig. 4. Sample locations between 'Flic-en-Flac' and Port-Louis (west coast).
Fig. 4. Localisation des échantillons entre Flic-en-Flac et Port-Louis (côte ouest).

Pour avoir une valeur de coprostanol représentative par rapport au pourcentage de carbone organique contenu dans le sédiment, les teneurs en coprostanol sont exprimées en pour-cent de carbone et rapportées aux teneurs de carbone organique total (%C-coprostanol/COTC). Exprimées en pourcentage de carbone, les fortes concentrations en coprostanol sont d' autant atténuées que les teneurs en matière organique sont aussi élevées, comme dans le cas des vasières riches en apports insulaires. Inversement, ces valeurs en pour-cent mettent en évidence certains sites où les teneurs en coprostanol restent élevées alors que celles en matière organique sont faibles, comme dans le cas des sédiments profonds.

La comparaison des teneurs en coprostanol permet donc d' identifier les régions les plus contaminées par les eaux usées autour de l' île.

- **Au large**

Sur la radiale de Port-Louis, les teneurs en coprostanol diminuent avec l' éloignement des côtes et la profondeur (Fig. 2). Au large du lagon de La Preneuse, par 190 m de profondeur, il persiste 0,9 mg/kg de coprostanol (soit 0,018% de C-coprostanol/COTC).

La teneur en coprostanol mesurée au niveau du collecteur d' eaux usées de Pointe Moyenne est de 0,6 mg/kg (soit 0.031% de C-coprostanol/COTC, prélèvement A6). A cet endroit, la teneur en coprostanol est relativement élevée par rapport à la quantité de matière organique (Fig. 4, Tabl. 2).

- **Dans les estuaires et les baies**

Dans la baie de Tamarin qui est bien brassée, car ouverte à la houle (Fig. 3, Tabl. 1), se rencontrent les teneurs les plus basses : le maximum n' est que de 0,38 mg/kg (soit 0.016% de C-coprostanol/COTC, prélèvement T17).

La contamination est plus élevée dans les autres estuaires, 1,1 mg/kg (soit 0.065% de C-coprostanol/COTC, prélèvement M23) sont mesurés à l' ouverture de la baie de Grande Rivière Noire. Le système "Rivière Noire" est complexe (Fig. 2 et 3, Tabl. 1). Les teneurs sont plus élevées dans le nord du chenal qui canalise les eaux de Grande Rivière Noire (1,2 mg/kg, prélèvement GN5) que dans le sud du chenal qui est soumis à l' influence des apports du lagon des Bénitiers (< 0,2 mg/kg, prélèvement S3). Une description des courants côtiers et de la bathymétrie est donnée dans la thèse de GENDRE (1992).

Les teneurs en coprostanol supérieures à 1,5 mg/kg sont caractéristiques des milieux les plus contaminés à Maurice. Par exemple, Elisabethville et Grand Baie (Fig. 5, Tabl. 3, prélèvements NW12 et NW1) qui sont des régions densément peuplées, montrent des teneurs en coprostanol élevées, soit respectivement 2,44 mg/kg et 1.9 mg/kg.

Un gradient décroissant des teneurs apparaît nettement quand on s' éloigne des estuaires de Grande Rivière du Nord-Ouest (Fig. 4, Tabl. 2) et de Grande Rivière du

Sud-Est (Fig. 6, Tabl. 4). La teneur mesurée à l' embouchure de Grande Rivière du Nord-Ouest est de 2,7 mg/kg (soit 0,012% de C-coprostanol/COTC) et celle mesurée devant l' embouchure de la Grande Rivière du Sud-Est est de 3 mg/kg (soit 0,019% de C-coprostanol/COTC). Les teneurs en matière organique dans ces sédiments sont aussi très élevées, ce qui abaisse les teneurs exprimées en pour-cent.

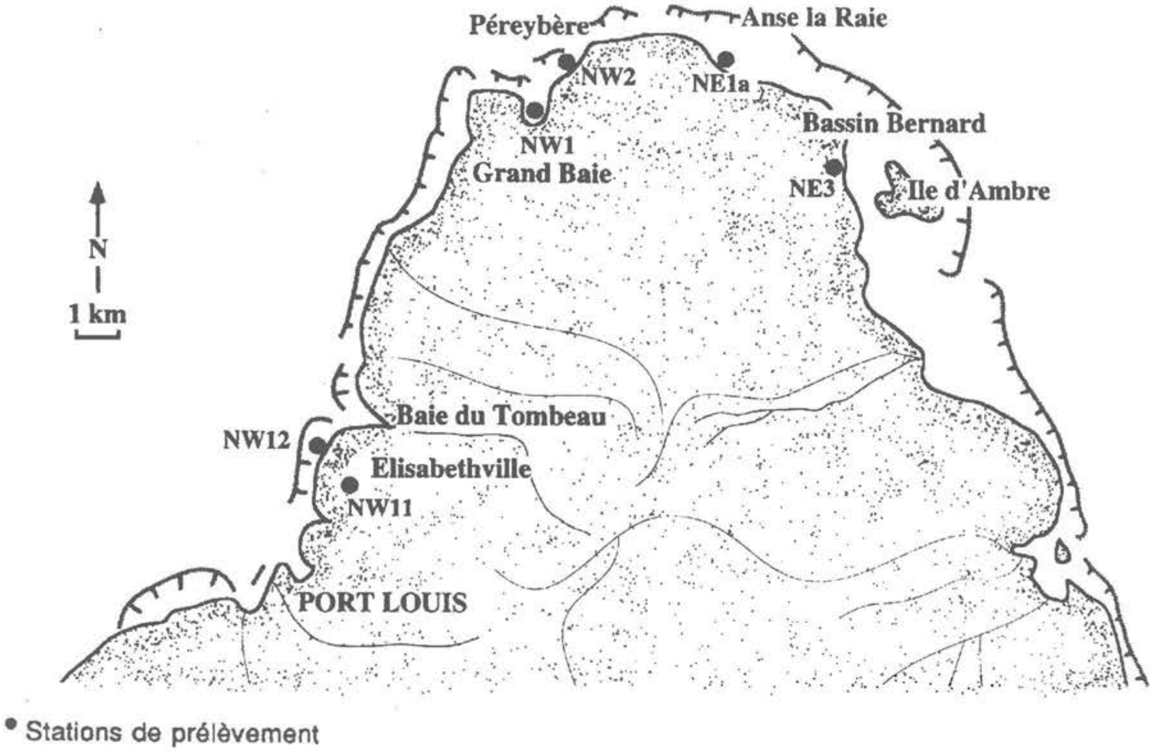

Fig. 5. Sample locations in the north.
Fig. 5. Localisation des échantillons dans le Nord.

- Dans les lagons

Les sédiments des lagons des Bénitiers (Fig. 3, Tabl. 1), de Trou d' Eau Douce et des Cerfs (Fig. 6, Tabl. 4) montrent localement des teneurs en coprostanol élevées (>1,5 mg/kg) :

- A l' ouest de l' île aux Bénitiers en arrière du récif barrière, 2 mg/kg (soit 0,15% de C-coprostanol/COTC, prélèvement BN1) sont mesurés dans un sable grossier bien oxydé et pauvre en matière organique (0.11% de COTC). Selon HATCHER *et al.* (1977), une telle teneur s' explique difficilement et paraît atypique.

- Dans la baie de la Petite Rivière Noire (Fig. 3, Tabl. 1), il a été mesuré 1,2 mg/kg (soit 0.019% de C-coprostanol/COTC, prélèvement PN1). Or, un élevage de cerfs est situé dans cette région et il pourrait être le facteur responsable de ces teneurs. Les eaux ruissellent dans les pâturages à faible pente et arrivent chargées dans le lagon. De plus, un grand élevage de bovins est situé au sud du Morne Brabant (Fig. 3, Tabl. 1) : les excréments des animaux sont directement rejetés dans le lagon où ils constituent une couche sur la plage et à la surface de l' eau (RUCH, observation

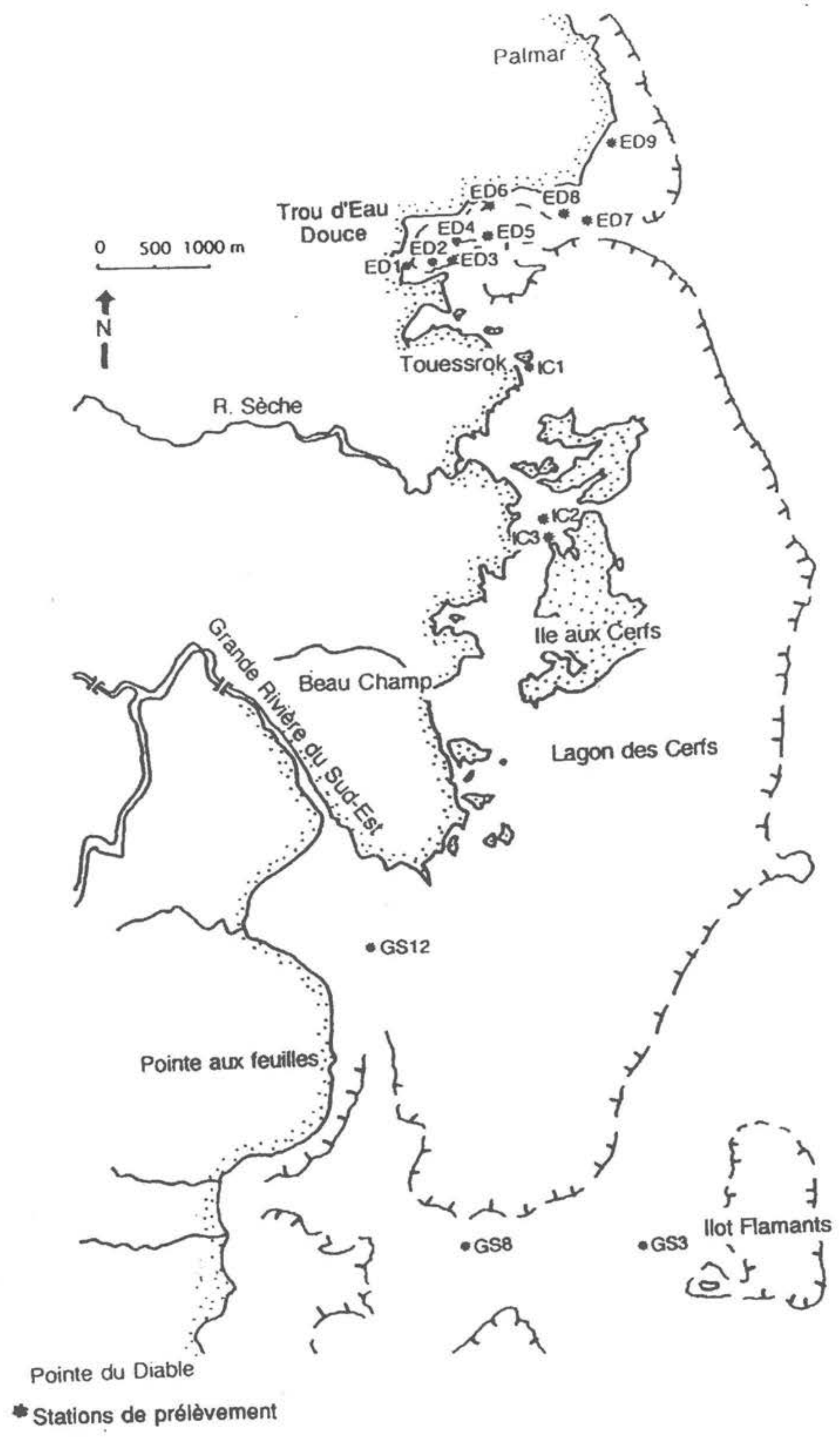

Fig. 6. Sample locations between 'la pointe du Diable' and 'Palmar' (east coast).
Fig. 6. Localisation des échantillons entre la pointe du Diable et Palmar (côte est).

avril-juillet 1990). Un autre élevage de cerfs est situé sur la pente nord du Morne Brabant.

Les 6 mg/kg de coprostanol mesurés dans la vasière derrière l' hôtel Méridien (prélèvement M1) ne représentent plus que 0,014% de C-coprostanol quand on les rapporte au carbone organique total. Ceci confirme l' origine autochtone de la matière organique dans ce fond de lagon. Comme il s' agit d' un lieu d' accumulation de matière organique (et donc tendant à l' anoxie), le coprostanol peut dériver du cholestérol d' origine autochtone (végétaux terrestres, algues, phytoplancton et zooplancton) par réduction bactérienne dans le sédiment (PITTET 1990).

La source principale de coprostanol étant à l' évidence les élevages qui bordent le lagon des Bénitiers, il est difficile d' évaluer l' impact des complexes hôteliers et de la population locale.

- Pour ce qui est des lagons de l' Est (Fig. 6, Tabl. 4), les 2,4 mg/kg (soit 0,11% de C-coprostanol/COTC, prélèvement IC1) mesurés devant l' arche de l' Hôtel Touessrok sont caractéristiques de l' impact hôtelier. Les 2,3 mg/kg (soit 0,19% de C-coprostanol/COTC) mesurés dans le chenal de Trou d' Eau Douce s' expliquent en partie par les courants qui drainent vers le large les eaux de la baie. La sortie du chenal de Trou d' Eau Douce est un point de confluence pour les eaux de l' Hôtel Touessrok et pour celles de la baie qui est entourée d' habitations.

4. CONCLUSION

La pollution par les eaux usées riches en éléments nutritifs a un impact non négligeable sur le littoral mauricien, ces eaux tendant à eutrophiser le milieu récifal (GENDRE *et al.* ce volume).

La pollution par les eaux usées révélée par les teneurs en coprostanol, apparaît sur tous les sédiments analysés. Elle est surtout importante dans les zones calmes des lagons où l' accumulation détritique est favorisée et près des embouchures des rivières; elle diminue avec l' éloignement des côtes et la profondeur des fonds.

Les teneurs en coprostanol > 1,5 mg/kg sont caractéristiques des milieux les plus contaminés. Elles se rencontrent à Grand Baie, dans la région d' Elisabethville, dans les estuaires de Grande Rivière du Nord-Ouest et de Grande Rivière du Sud-Est, près de l' hôtel Touessrok et à la sortie du chenal de Trou d' Eau Douce.

REMERCIEMENTS - Nous remercions tous les scientifiques qui ont participé à cette étude des écosystèmes littoraux de l' île Maurice et en particulier M.J. MULLER qui a dirigé le projet.
Ce travail fut possible grâce aux supports financiers de la Commission des Communautés Européennes (projets 946/1988 et 946/1989) et du Fonds National Suisse de la Recherche Scientifique (projet 21.26147.89). Nous remercions aussi, à Maurice, les Ministères du Plan et de l' Environnement, le Collège des Sciences, le bureau d' ingénieurs Sigma et la Central Water Authority pour leur collaboration.

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Tableau 1 :

NOMS	PROF. (m)	COA %	CORT %	COTC %	COPRO mg kg^{-1}	% C-copro / COTC
M1	- 1	0.67	2.85	3.53	6.00	0.014
S1	- 1	0.18	0.17	0.35	0.58	0.014
S2	- 1	0.29	0.37	0.66	0.37	0.005
S5	- 1	0.30	0.58	0.88	<0.20	0.001
PN1	- 1	0.12	0.42	0.54	1.20	0.019
BN1	- 1	0.11	0.00	0.11	2.00	0.152
BN2	- 1	0.20	0.00	0.20	1.10	0.046
BN3	- 1	0.18	0.00	0.18	1.20	0.056
R1	-25	0.11	0.09	0.20	0.80	0.034
R3	-10	0.17	0.34	0.51	0.37	0.006
R4	- 6	0.00	0.22	0.22	0.25	0.010
R5	- 3	0.34	1.95	2.29	0.80	0.003
R6	- 1	0.09	0.11	0.20	0.82	0.034
C10	-60	0.14	0.27	0.41	0.53	0.011
C11	-70	0.13	0.25	0.38	0.38	0.008
C13	-90	0.11	0.27	0.38	0.89	0.020
M20	-166	0.12	0.29	0.41	0.47	0.010
M21	-65	0.14	0.34	0.48	0.32	0.006
M23	-45	0.10	0.04	0.14	1.10	0.065
S3	-30	0.12	0.00	0.12	<0.20	0.007
GN3	-10	0.20	1.37	1.57	1.00	0.005
GN5	-30	0.16	0.39	0.55	1.20	0.018
L2	-120	0.11	0.23	0.34	0.89	0.022
L2'	-100	0.12	0.24	0.36	0.90	0.021
L3	-142	0.14	0.44	0.58	0.31	0.004
L4	-190	0.10	0.33	0.43	0.94	0.018
T7	- 4	0.07	0.01	0.08	<0.20	0.011
T8	- 9	0.10	0.03	0.13	0.25	0.016
T9	-10	0.13	0.05	0.18	<0.20	0.005
T10	-15	0.13	0.07	0.20	<0.20	0.004
T11	-16	0.12	0.10	0.22	<0.20	0.004
T14	-19	0.12	0.09	0.21	<0.20	0.004
T15	-23	0.13	0.06	0.19	0.20	0.009
T16	-21	0.13	0.04	0.17	<0.20	0.005
T17	-33	0.15	0.05	0.20	0.38	0.016
T19	-55	0.15	0.08	0.23	<0.20	0.004
T21	-80	0.11	0.11	0.22	0.32	0.012

Table 1 - The parameters of organic matter measured between the 'Morne Brabant' and 'Flic-en-Flac' in the west coast (see figure 3) : Percentage of Soluble Organic Carbon (COA), percentage of Organic Carbon of the total Rock = Insoluble Organic Carbon (CORT), total Organic Carbon (COTC), Coprostanol content in mg kg^{-1} (COPRO), percentage of Carbon of coprostanol in comparison with the total organic carbon (%C-copro/COTC).

Tableau 1 - Les paramètres de la matière organique mesurés entre le Morne Brabant et Flic-en-Flac sur la côte ouest (voir figure 3): pourcentage de Carbone Organique Acidosoluble (COA), pourcentage de Carbone Organique du sédiment total = Carbone Organique Insoluble (CORT), Carbone Organique Total (COTC), teneur en Coprostanol en mg kg^{-1} (COPRO), pourcentage de Carbone du Coprostanol par rapport au Carbone Organique Total (%C-copro/COTC).

Tableau 2 :

NOMS	PROF. (m)	COA %	CORT %	COTC %	COPRO mg kg^{-1}	% C-copro / COTC
A6	-50	0.09	0.08	0.17	0.63	0.031
A9	-8	0.20	1.60	1.80	2.70	0.012
A11	-17	0.57	2.48	3.05	1.70	0.005
A13	-31	0.11	0.63	0.74	0.44	0.005
A14	-53	0.17	0.95	1.12	1.75	0.013

Table 2 - The parameters of organic matter measured between 'Flic-en-Flac' and 'Port-Louis' in the west coast (see figure 4).

Tableau 2 - Les paramètres de la matière organique mesurés entre Flic-en-Flac et Port-Louis sur la côte ouest (voir figure 4).

Tableau 3 :

NOMS	PROF. (m)	COA %	CORT %	COTC %	COPRO mg kg^{-1}	% C-copro / COTC
NW11	0	0.61	1.91	2.52	0.78	0.002
NW12	-0.3	0.24	0.93	1.17	2.44	0.017
NW1	-3.5	0.21	0.29	0.50	1.90	0.032
NW2	-4	0.13	0.00	0.13	0.51	0.032
NE1a	-2	0.15	0.46	0.61	3.05	0.042
NE3	0	0.64	2.87	3.52	1.45	0.003

Table 3 - The parameters of organic matter measured in the north (see figure 5).

Tableau 3 - Les paramètres de la matière organique mesurés dans le Nord (voir figure 5).

Tableau 4 :

NOMS	PROF. (m)	COA %	CORT %	COTC %	COPRO mg kg^{-1}	% C-copro / COTC
ED1	-5	0.21	0.19	0.40	0.52	0.011
ED2	-10	0.25	0.23	0.48	0.70	0.012
ED3	-10	0.27	0.23	0.50	0.76	0.013
ED4	-12	0.16	0.12	0.28	0.80	0.024
ED5	-12	0.35	0.55	0.90	0.60	0.006
ED6	-5	0.16	0.00	0.16	0.58	0.030
ED7	-9	0.10	0.00	0.10	2.34	0.195
ED8	-12	0.18	0.19	0.37	0.48	0.011
ED9	-2	0.13	0.00	0.13	0.46	0.029
IC1	-1	0.18	0.00	0.18	2.40	0.111
IC2	-5	0.18	0.07	0.25	0.40	0.013
IC3	-3	0.13	0.00	0.13	0.50	0.032
GS3	-25	0.20	0.20	0.40	1.70	0.036
GS8	-11	0.17	0.19	0.36	2.10	0.048
GS12	-2	0.43	0.92	1.35	3.00	0.019

Table 4 - The parameters of organic matter measured between the 'pointe du Diable' and 'Palmar' in the east coast (see figure 6).

Tableau 4 - Les paramètres de la matière organique mesurés entre la pointe du Diable et Palmar sur la côte est (voir figure 6).

VARIATIONS IN BIOEROSION ACROSS A MIOCENE REEF SYSTEM, MALLORCA, SPAIN: A POTENTIAL PALAEOENVIRONMENTAL TOOL AND MORE..!

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Abstract - Macroboring organisms have been widely recognized as important agents of framework destruction and alteration within both modern and ancient reef environments. Relatively little is known however about variations in the distribution of such organisms (principally sponges, bivalves and worms) within individual reefs, and in particular within fossil reefs. The Upper Miocene reefs, exposed around the south-east coast of Mallorca, have presented a unique opportunity in which to assess variations in both the distribution of framework borers, and the intensity of boring activity in different parts of the reef system. The distribution of individual bore morphologies are observed to be highly variable across the reef, although different parts of the reef system can be characterized based on the abundance of specific groups of borers. The highest diversity and abundance of borers is observed within back-reef and lagoonal facies. The distribution of boring organisms across the reef appears to be closely linked to the morphology and structure of the reef framebuilders. Massive corals are always more extensively bored, and contain a higher diversity of boring organisms than branched or platy corals. Locally, factors such as sediment accumulation rate and degree of substrate encrustation appear to have exerted some additional influence. The recognition of different associations of boring organisms in different parts of the reef not only has potential as a useful palaeoenvironmental tool, but has implications for our understanding of rates of reef accretion. Since reef accretion will be significantly influenced by the rate at which reef framework is broken down, the abundance of different boring organisms, and the response of different framebuilders to boring activity is of considerable importance. Plate-like or branched corals, whilst typically less intensely bored, will be highly vulnerable to the effects of boring activity. In contrast, the more intensely bored, but volumetrically larger coral morphologies, are more capable of surviving such damage. This preservational bias has important implications for our understanding of accretion rates and styles of preservation in both modern and fossil reef systems.

1. INTRODUCTION

The importance of bioerosion as a key process in the reef environment is now well established (GOREAU & HARTMAN 1963; HEIN & RISK 1975; BROMLEY 1978; MACINTYRE 1984), both in terms of its role as a modifier of reef framework and as a major source of reefal sediment. Grazing activity is perhaps, to anyone swimming over a reef, the most visibly apparent of such processes. However, of at least equal importance (in terms of reef destruction) are the activities of the endolithic organisms, such as sponges, bivalves and worms which bore into the coral framework. This essentially hidden community plays a major role in modifying and breaking down considerable amounts of primary reef carbonate, and as such must be regarded as a key process affecting the development and accretion of reef systems (HALLOCK 1988). Despite the recognition of boring activity as an important process within the reef environment, relatively little is known about how the distribution of different boring organisms varies within individual reef systems, and how these distributional patterns relate to variations in substrate morphology and structure, and the local environmental conditions. The Upper Miocene reefs of Mallorca have presented a unique opportunity in which to assess such distributional variations. Leaching of the originally aragonitic coral skeletons by meteoric waters has permitted recognition of borings, which were infilled with sediment and lithified, prior to dissolution of the coral framework. These borings are preserved as 3-dimensional casts and typically exhibit highly characteristic morphologies, enabling classification (usually to ichnospecies level) and comparison with the borings produced in modern reef environments. It has thus been possible to identify changes both in the composition of the boring community and the intensity of boring activity across the reef system. The Mallorcan reefs are constructed of no more than three species of coral, and have a clearly defined distribution of coral morphologies, that reflect variations in depth and wave energy across the reef. They therefore present an insight into the nature and distribution of a reef boring community.

2. STUDY AREA

Mallorca, the largest of the Balearic Islands, is situated in the western Mediterranean and deposits of Upper Miocene reef and reef-related facies are particularly well exposed around the south and south-eastern parts of the island (Fig. 1).

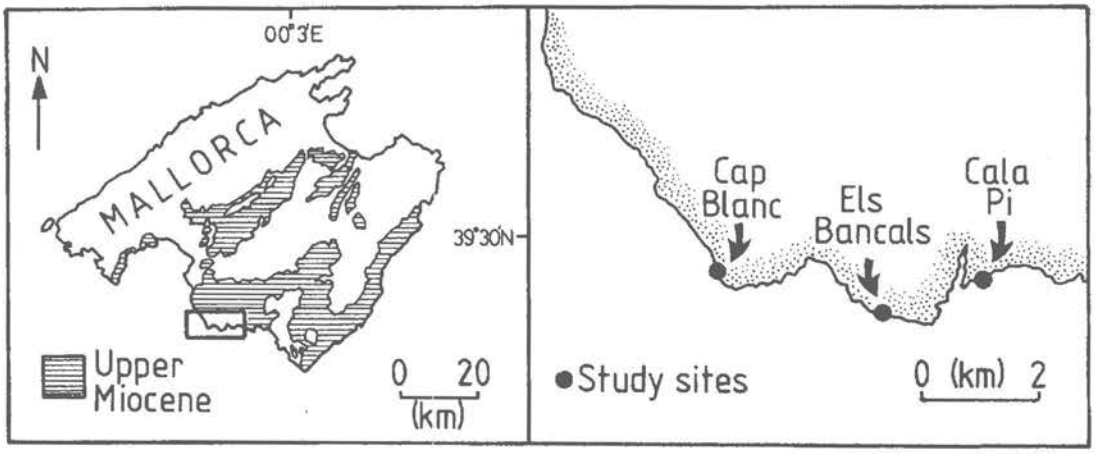

Fig. 1. Location map showing location of study sites on Mallorca

The reefs represent the products of a progradational platform that developed during the late Tortonian-early Messinian, and comprise a complex sequence of vertically shifting reef units and erosional surfaces, which developed in response to a series of high-frequency sea-level fluctuations (POMAR 1991; POMAR & WARD 1994). Coral diversity in the reefs is low (the causes of which are somewhat controversial and beyond discussion here), and although *Porites, Tarbellastraea* and *Siderastrea* are reported in the earlier reef units, *Porites* alone dominates the coral assemblage in the youngest reefs (ESTEBAN 1980). Of most significance is the fact that reduced coral diversity had no apparent effect on the size of the reefs (ESTEBAN 1980), with the *Porites* assuming a variety of depth dependant morphologies. Reef-front facies exhibit a transition from plate-like coral forms at the base of the reef, through stick or branched corals in the middle sections of the reef, to large coral head morphologies approaching the reef crest. The back-reef coral facies exhibit a typically columnar or pillar-like morphology, whilst the lagoonal facies comprise patch reefs constructed of large hemispherical corals (POMAR *et al.* 1985).

3. METHODS

Study sites were chosen at Cap Blanc, Els Bancals and Cala Pi (Fig. 1), that permitted access to reef-front, back-reef and lagoonal facies respectively. At Cap Blanc (reef-front facies), three vertical transect lines were established (approx. 100m to west of the lighthouse), from which all morphological zones on the reef could be studied. From these vertical lines, shorter lateral transects (5-6m) were taken every 4-5m (depending on accessibility), along which all in-situ coral framework was examined. Exposures at Els Bancals (back-reef) and at Cala Pi (lagoonal patch reefs), outcrop along horizontal cliff sections, and lateral traverses of these sections were made. Despite the back-reef and lagoonal facies being of a slightly older age than the reef-front facies, many of the styles of borings observed were found to be consistent throughout the reef sequence, and thus the comparisons made between intra-reef settings are taken to be valid. At each locality, individual corals (that had the potential for borings to be exposed) were examined, and coral morphology, species type, coral dimensions and presence or absence of borings was noted. Where borings were observed they were assigned to an ichnospecies on the basis of bore morphology, their % abundance in relation to all other borings in the coral was noted, and the total % of coral surface area bored was estimated and recorded. In total nearly 900 individual coral heads were examined, 719 on the reef-front, 89 in the back-reef and 73 in the lagoonal facies.

4. DISTRIBUTION OF ICHNOSPECIES

Within the Mallorcan reefs the borings produced by sponges, bivalves and worms are preserved as 3-dimensional casts within the moulds of the former corals. Identification and classification of borings has been based on the morphological descriptions of such ichnofaunas that have been given by BROMLEY (1970), WARME (1975), BROMLEY & D' ALESSANDRO (1983;1984), KELLY & BROMLEY (1984) and PLEYDELL & JONES (1988). Twelve styles of bore morphology were identified, of which 8 species belonged to the ichnogenus *Entobia*, 2 to the ichnogenus *Gastrochaenolites*, and 1 each to the ichnogenera *Maeandropolydora* and *Trypanites* (Fig. 2). Distributional patterns of individual ichnospecies are observed to be highly variable across the reef (Fig. 3). Some ichnospecies (*eg. Entobia ovula*) are common throughout the reef, whilst other ichnospecies (*eg. Entobia megastoma*) appear to show a marked preference for specific sites. It is apparent that both the diversity of boring organisms and the amount of boring activity (in terms of the ratio of bored : non-bored corals and the % of coral surface area bored) increases from lower to upper reef-front sites, but is observed to be highest within the back-reef and lagoonal sites. Initial attempts to characterize the zonation of bores were confused because many of the bore morphologies observed are present throughout the reef system. A more useful zonation is obtained by assessing the distribution of different groups of borers (sponges, bivalves and worms) across the reef as a whole.

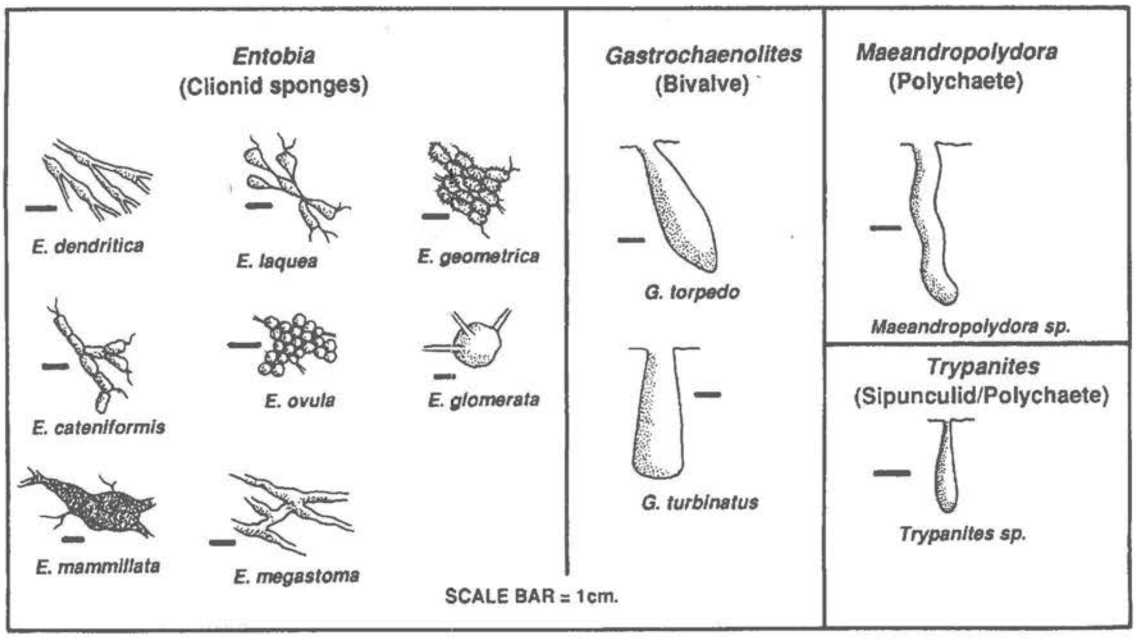

Fig. 2. Ichnospecies identified within the Mallorcan reef system.

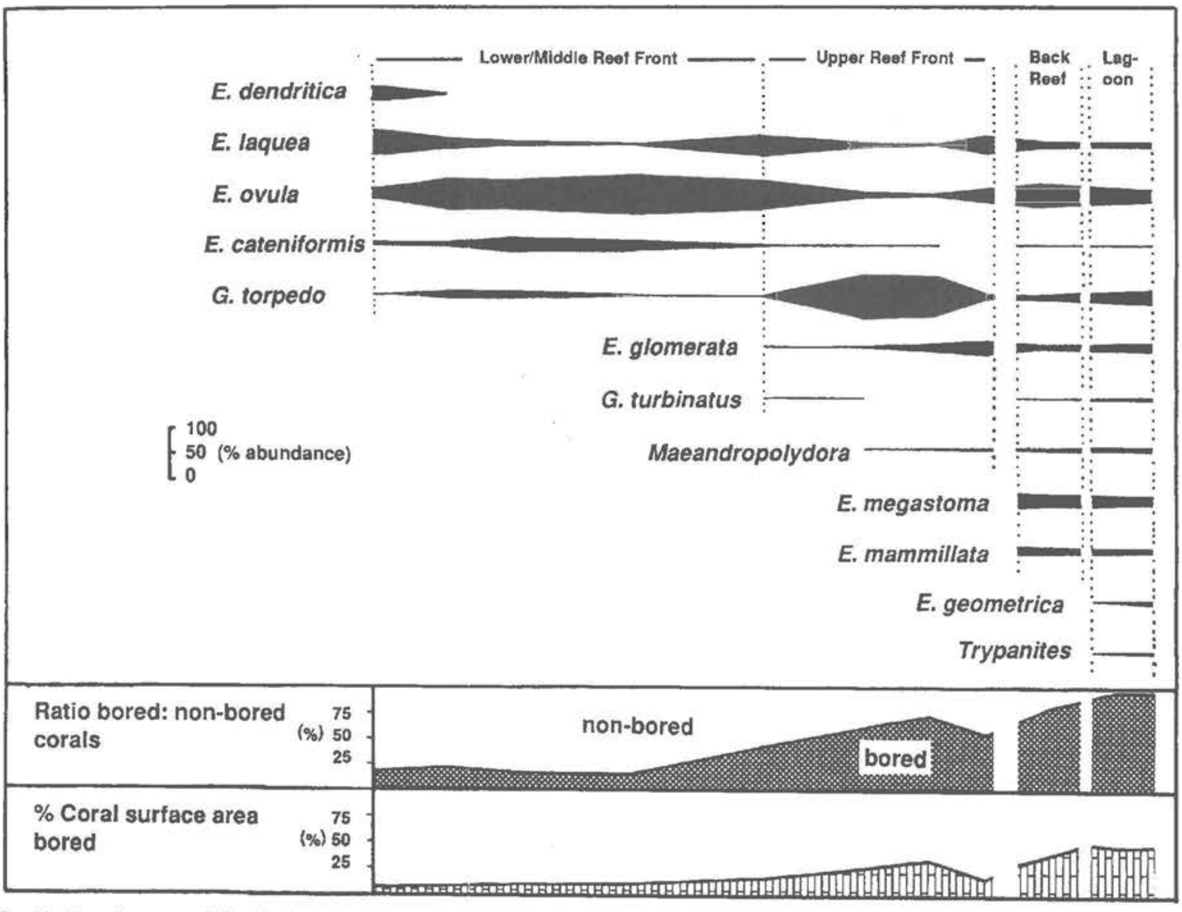

Fig. 3. Abundance and distribution of ichnospecies across the Mallorcan reef system.

This has allowed the recognition of four distinct associations of boring organisms that characterize specific parts of the reef system. Association 1, which characterizes the lower and middle parts of the reef-front, contains a low diversity and abundance of borers, in which the *Entobia* (sponge borings) represent the most common style of boring morphology. Association 2 characterizes the upper reef-front, and is dominated by bivalve boring activity, though sponges are locally also important. Abundance and diversity of borers and the intensity of boring activity is typically much higher than in lower parts of the reef. This is largely attributed to the existence of a live-coral boring association between the bivalve *Lithophaga* and the coral *Porites*, enabling the *Lithophaga* to exploit a much greater amount of substrate than would otherwise be available. The *Lithophaga* exhibit complex back-fill structures (anterior boring linings) characteristic of live-coral boring bivalves. Association 3, characterising the columnar corals of the back-reef, is again dominated by sponge boring activity, though abundance and diversity are much higher than previously observed. Bivalve and worm boring activity is of limited importance. Association 4, contains the highest diversity and abundance of borers from anywhere in the reef system, and is characteristic of the lagoonal patch-reefs. Sponges are again dominant, though bivalves are also common, and worm boring activity is more common than in any other part of the reef system. However, although intensity of boring activity appears to be higher in the lagoon than in other parts of the reef, volumetrically the greatest amount of boring activity occurred within the coral heads of the upper reef-front, where the depth of bore penetration, by for example *G. torpedo* (up to 120mm in length), exceeds anything observed within the lagoon corals.

The distribution of boring organisms across the Mallorcan reefs appears to have been primarily controlled by the structure and morphology of the reef framebuilders. Although shallower parts of the reef system do contain both a high diversity and abundance of borers, there is no evidence to indicate that bathymetry or hydraulic energy levels acted as the primary controls (BROMLEY 1978) to boring organism distribution. Broadly similar assemblages can be observed within both high energy upper reef-front facies, and within quiet water lagoonal facies. Furthermore, the wide distribution of many of the borers across the reefs is evidence against any tight bathymetric limitation. Of more obvious importance is the structure and morphology of the framebuilders themselves. This should perhaps be expected however, since reef boring organisms live within the coral substrate, and are thus directly affected by substrate morphology, structure and growth rate. Substrate morphology acts as a major control by influencing the amount of dead, exposed substrate available to the boring organisms (MacGEACHY & STEARN 1976) in relation to the volume of the coral substrate. Thus, massive coral heads will potentially present much greater amounts of available substrate to boring organisms than branched or stick corals. Furthermore, massive corals exert little or no limitation on the size of borings that can be produced, so that whilst small chambered borings are commonly widely distributed across reef systems, the larger bore morphologies are restricted only to the larger coral morphologies.

Varying skeletal density and structure between species acts as a further potential control, most directly by influencing boring strategy. This is most apparent within the Mallorcan reefs if early and late stages of sponge chamber development are compared. Early, exploratory threads within sponge borings appear to be most strongly influenced by the internal structure of the corals, and are typically developed in the less dense, intra-corallite areas. There is also evidence of a coral species preference between borers within the lagoonal coral facies where several species of corals coexist. These colonies typically have similar growth morphologies, but the species *Siderastrea* and particularly *Tarbellastraea* always appear more intensely bored than colonies of *Porites*. This may well reflect increased skeletal densities in the two former species, the denser corals being preferred by the boring organisms (see HIGHSMITH 1981, and RICE & MACINTYRE 1982, who have made similar observations). A final control that should be considered is the role of coral growth rates, or more specifically, coral growth rate in relation to sediment accumulation rates. Growth rate will determine, to an extent, the amount of substrate available, into which organisms can bore, but this will also be influenced by the frequency of coral death and the rate at which sediments accumulate on and around the reef. Preservation of corals will be enhanced when sediment accumulation rates are high and thus bioerosion rates low. Conversely, if sediment accumulates at a slow rate, coral will be exposed to the destructive effects of boring for increased periods of time, and thus preservation can be expected to be poor.

5. IMPLICATIONS FOR THE FOSSIL RECORD

It is apparent that different coral morphologies will be bored by different groups of boring organisms, and that the primary control on the nature of the boring community will be the structure and morphology of the reef framework itself. An understanding of variations in the distribution of boring organisms, and associations of boring organisms across different parts of a reef system thus presents us with a potentially useful tool for palaeoenvironmental reconstruction work. However, there is also significant potential to use this data to improve our understanding of variations in the rates and styles of framework destruction within reefs. Rates of substrate destruction will depend, not only on the nature and size of the borings that these organisms produce, but also on the impact that such activity has on the corals themselves. It would appear that whilst branched or stick corals typically contain lower diversities and abundances of borers than more massive corals, they are also more prone to the effects of such boring activity (primarily through skeletal weakening, and thus physical destruction). Larger coral heads by contrast, though more extensively bored, are also more capable of surviving boring activity, and are thus likely to be preferentially preserved. Rates of reef accretion will thus potentially be highest in areas constructed primarily of larger head corals, where accretion will occur through the direct overgrowth of coral. In areas dominated by more delicate corals, high turnover rates, due to breakdown and destruction mean that accretion rates will

potentially be lower, with new framework accommodating newly created space on the reef.
Such a preservational bias has obvious implications in terms of our interpretation of modern and ancient reef systems. It must be stressed however, that the Miocene reefs on Mallorca are essentially very 'simplistic', being constructed of only a few coral species and exhibiting a clearly defined morphological zonation. Modern reefs, are both more complex in construction and more diverse in terms of coral species. However, the data from the Mallorcan reefs is acting as a guide for future work both on the distribution of boring organisms within reefs, and the potential effects of bioerosion on the development and preservation of reef communities.

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CORAL REEFS IN THE GULF - 2 YEARS AFTER THE GULF WAR OIL SPILL

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Abstract -In January 1991, at the end of the Gulf War, Iraqi troops released the largest oil spill ever recorded into the marine environment of the Persian/Arabian Gulf. At the same time, more than 500 oil wells were set ablaze, threatening to change the climatic environment in which the coral reefs exist.

In August-October 1991, an early assessment of the expected damage was conducted from aboard the MV Greenpeace. This allowed some reefs, investigated by other researchers before the Gulf War, to be revisited. Sections of coral reefs in Bahrain, Saudi Arabia, Kuwait and Iran were recorded with the use of an underwater video system. In none of the reefs were there any signs of oil coverage or bleaching, nor were abnormally high numbers of dead corals observed. Comparison with the results of earlier investigations showed little change.

In order to detect any changes that may have occurred as late effects of the oil spill, 10 permanent study sites were established on Saudi Arabian inshore and offshore reefs. Comparison of the live coral cover between June 1992-July 1993 showed a limited change, with no signs of coral cover deterioration.

Although, no signs of damage were visible in the Kuwaiti reefs in September 1991, some researchers observed large numbers of bleached or dead corals. Subsequently investigations by other workers concluded that the extent of the damage was initially overestimated, and that the reefs were already in a state of recovery. A link between the oil spill and the documented reef impact could not be proven.

1. INTRODUCTION

At the end of the Gulf War, Iraqi troops released 6-8 million barrels of crude oil from various sources into the marine environment of the Persian/Arabian Gulf (McKINNON & VINE 1991; DOWNING 1992; ROBERTS *et al.* 1993). The largest oil spill on record drifted southward towards the Kuwaiti and Saudi Arabian coral reefs. In addition to this threat, there was major concern that the reefs had suffered due to the climatic changes caused by the large number of burning oil wells with an estimated emission of 500 million barrels (READMAN *et al.* 1992) to 1.12 billion barrels (SADIQ & McCAIN 1993).

The corals in the Gulf are especially vulnerable to temperature reductions because they occur in a region with extreme cold winter water temperatures. Even natural temperature fluctuations prior to the Gulf War led to a severe number of mortalities amongst some coral species (COLES & FADLALLAH 1991).

Despite the fear of a major disaster, scientific investigations of the ecological consequences of the Gulf War began late, because they had to be conducted in previous war zones. Amongst the first to investigate the damage was an international

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team of scientists sent by Greenpeace. About six months after the Gulf War, the team including researchers from the Gulf states commenced their investigations from aboard the MV Greenpeace (GREENPEACE 1992). During the two months voyage through the northern part of the Gulf (Fig. 1) the first assessment of the health of the coral reefs in Saudi Arabia, Kuwait, Iran and Bahrain was conducted (VOGT 1991). Selected parts of some reefs were investigated using a manta board (DONE *et al.* 1981, MORAN *et al.* 1989), the line transect method (LOYA 1978) as well as a method using underwater video recordings (VOGT 1995).

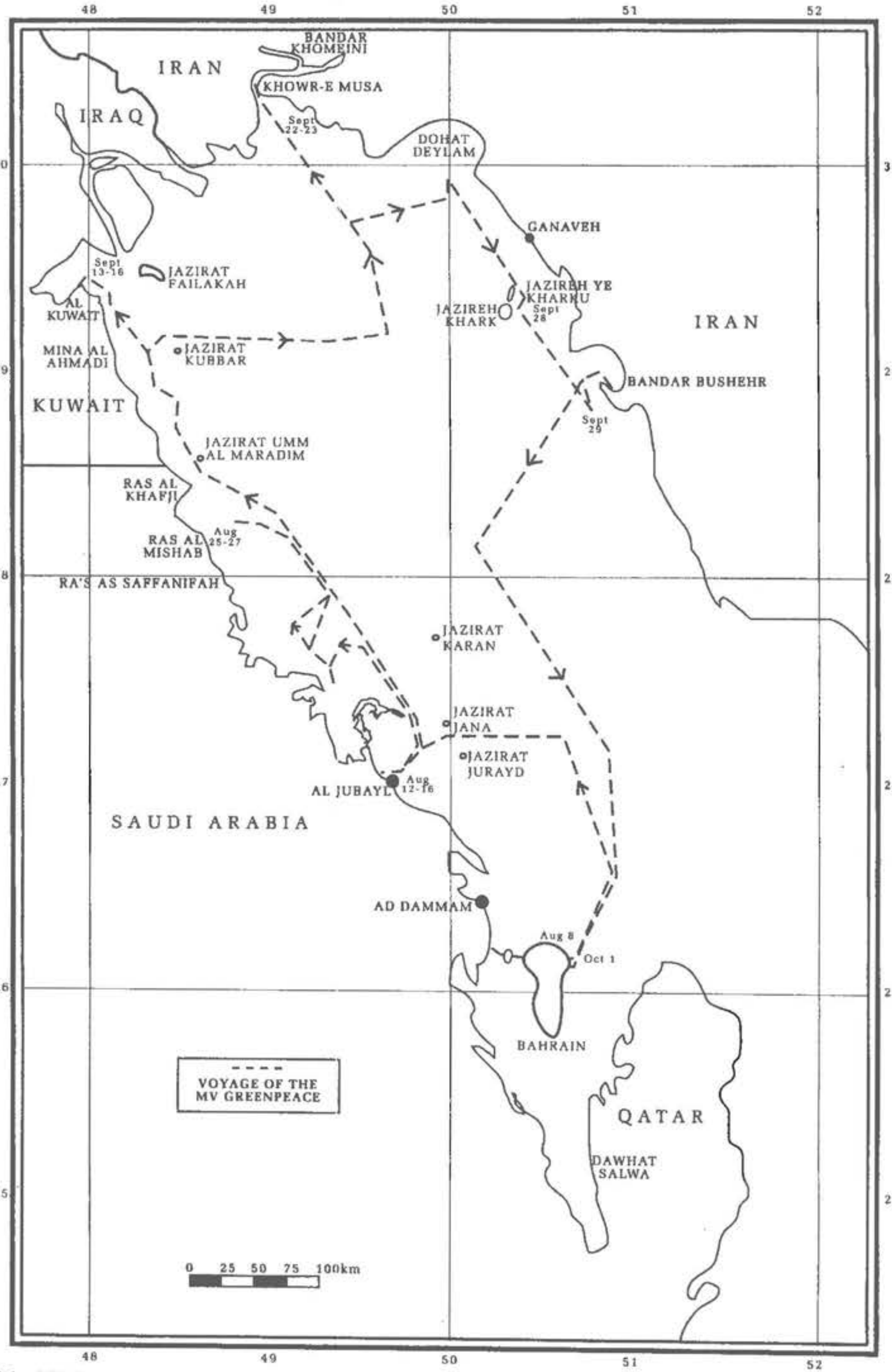
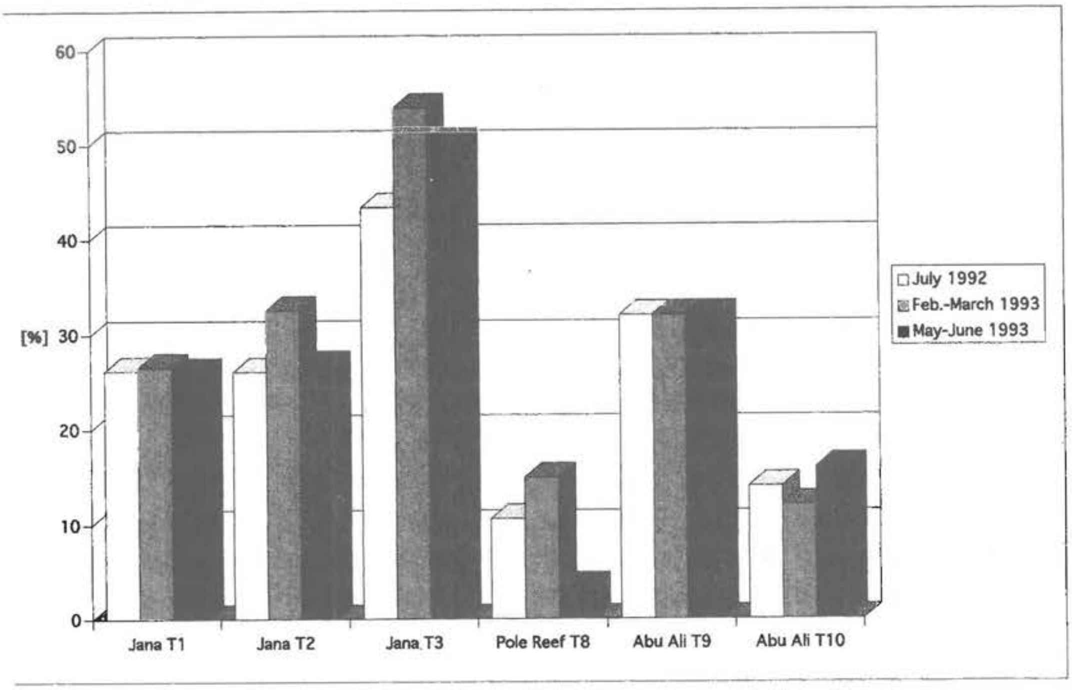


Fig. 1. Voyage of the MV Greenpeace during August-October 1991 (from Greenpeace 1992)

2. SAUDI ARABIA

In Saudi Arabia numerous patch reefs and coral communities along the coastlines were visited, including the fringing reef off the heavily oiled coastline of Abu Ali. More detailed investigations were conducted at some patch reefs previously investigated, (McCAIN *et al.* 1984; KFUMP/RI 1992) in order to detect any changes that may have been related to the oil spill. In Manifa Bay sections of the reefs named A, B and F by McCAIN *et al.* (1984) were recorded with an underwater video camera. Live coral cover within 20 squares of 0,25 cm^2 were calculated for each reef flat using digital video analysis (VOGT 1994). In August 1991, live coral cover consisting exclusively of *Porites compressa* was high at all three reefs (A = 59 %, B = 85 % and F = 71 %). Due to different methods of investigation, different sample size and sample areas, a comparison using statistical tests appears to be inappropriate. However, estimations of the maximum live coral cover before the Gulf War by McCAIN *et al.* (1984) were lower for the reefs A and B and only slightly higher for reef F (A = 50%, B = 30 % and F = 80 %). Although these data cannot be compared without caution, they indicate that live coral cover was high before and after the Gulf War. Furthermore the absence of any signs of bleached or diseased corals suggests that the oil spill caused no visible damage to the corals. Similar conclusions were made by KFUPM/RI (1992) after conducting surveys at the same reefs between March and October 1991. Although in March 1991 oil sheen was still drifting over the shallow reefs, KFUPM/RI (1992) concluded that there was no evidence of any impact on the corals from the oil spill. COLES & FADLALLAH (1991) reported that all *Acropora* species in Manifa Bay were killed due to the extremely cold water temperatures during the winter of 1988/89. Two years later no new settlements of *Acropora* were found during this study.

About 6 months after the oil was released, there were no signs of any impact in the coral reefs or coral communities in Saudi Arabia (VOGT 1991; GREENPEACE 1992). In order to detect changes that may have occurred as late effects, 10 permanent transect lines of 50 m in length were laid out at some offshore and inshore reefs (VOGT 1994 a, b). Between July 1992 and June 1993, the transects were filmed up to three times with a video camera. More than 1500 video images were digitised and all the species were outlined and their areas calculated using a computer image analysis system. The results indicated that the live coral cover at these selected inshore and offshore reefs were in a stable state with very limited changes (Fig. 2). In June/July 1994 most of the transects were visited for a fourth time, completing 2 years of monitoring (VOGT & AL-KHUZAYIM 1994). This most recent survey indicated that more than 3 years after the oil releases, the coral reefs investigated in Saudi Arabia were in a stable state with no signs of any late effects from the Gulf War oil spill. Further studies also failed to detect any impact that could be related to the Gulf War oil spill (FADLALLAH *et al.* 1993 a; DOWNING & ROBERTS 1993; ROBERTS 1993).



Standard deviations: T1: 0,27, T2: 3,55, T3: 5,33, T8: 5,82, T9: 0,00, T10: 2,00
Fig. 2. Live coral cover at 3 offshore (T 1-3) and 3 inshore (T 8-10 reefs in Saudi Arabia between July 1992 and June 1993

3. KUWAIT

In July 1991, DOWNING (1991) reported that various reefs in Kuwait were healthy, however, water temperatures were lower than in preceding years. In September 1991, video recordings were taken at the Kuwaiti coral reefs surrounding the islands of Umm Al-Maradum and Kubbar. The reefs at both islands appeared to be in a healthy state with high live coral cover of 60 and 68% respectively. The predominant coral genera were *Acropora* and *Porites* at Kubbar and *Acropora* at Umm Al-Maradum. No signs of dead or dying corals were observed. However, after the winter 1991/92, FADLALLAH *et al.* (1993a) observed in May 1992 that many corals showed clear signs of stress. At the two reefs investigated, numerous corals were found to have been recently killed or bleached. In a summary FADLALLAH *et al.* (1993b) stated that numerous corals at Kubbar Island were also dead, bleached or dying. These findings led to a subsequent investigation by DOWNING & ROBERTS (1993 a; b) who revisited those reefs and the offshore reefs. However, the damage occurred in a patchy distribution. Although the authors could not confirm widespread coral death, some impact was clearly visible. At almost all locations visited recovery of the affected colonies was well underway.

4. IRAN AND BAHRAIN

The MV Greenpeace cruise also provided the opportunity to take recordings of coral reefs in Iran and Bahrain. As it turned out during the voyage, the Gulf War oil spill did not reach the reefs of these countries. All recordings were taken before the winter, therefore no impact was expected due to climatic changes. Therefore the results of these investigations will be reported elsewhere.

5. CONCLUSIONS

The Gulf War oil spill was the so far largest oil spill on record (6-8 million barrels or 0.86-1.1 million t) which affected a 707 km long coastline (GUNDLACH *et al.* 1993). In comparison the Exxon Valdez (33 000 t) oiled more than 1700 km coastline, Amoco Cadiz (223 000 t) 375 km (GUNDLACH *et al.* 1993) and Bahia Las Minas (50-100 000 barrels (BURNS & KNAP 1989 ; CUBIT & CONNOR 1993) or 7-14 000 t 82 km of shoreline (JACKSON *et al.* 1989). The extent of the shoreline affected could have been much larger considering the size of the Gulf War oil spill. However, the damages were most severely affecting bird populations, mangrove areas, salt marshes and the flora and fauna of the intertidal (GRAINGER 1991; GERGES 1993).

After the winter 1991/92, some coral reefs in Kuwait showed clear signs of distress, however the impact occurred at a few reefs only whereas others appeared to be healthy. The patchy distribution of the damages made an explanation extremely difficult. DOWNING (1992) and DOWNING & ROBERTS (1993) suggested a complex of causal factors including reduced winter water temperatures, the shading effect of the plumes caused by the burning oil wells and toxic effects of fresh crude oil flowing over the reefs. However, the authors concluded that it is highly unlikely that Gulf War pollution was the only cause for the observed coral death. In the past low winter water temperatures were responsible for extensive coral mortalities in the Gulf (COLES & FADLALLAH 1991) and it cannot be ruled out that natural events may have played a key role. Overall the coral reefs in the Gulf survived the oil spill and the consequences of the burning oil wells remarkably unscathed with no detectable damages in most of the reefs.

However, a previous oil spill of comparably minor size (50-100 000 barrels) caused severe coral death in areas of 0-3 m water depth (BURNS & KNAP 1989 ; JACKSON *et al.* 1989 ; CUBIT & CONNOR 1993). The difference between the consequences of the Bahia Las Minas oil spill and the Gulf War oil spill may lay in the fact that in the Panamanian reefs, organisms were immersed in oil during extreme low tides and the substratum was coated in oil (CUBIT & CONNOR 1993). In the Gulf, however, nothing similar was observed and it appears that although the water layer between the oil and the corals was in some areas less than one metre thick, this was sufficient to avoid large scale coral death.

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Photo 1: More than six months after the oil wells were set ablaze, the plume of the remaining fires still darken the sky over Kuwait City (Photo T. Henningsen).

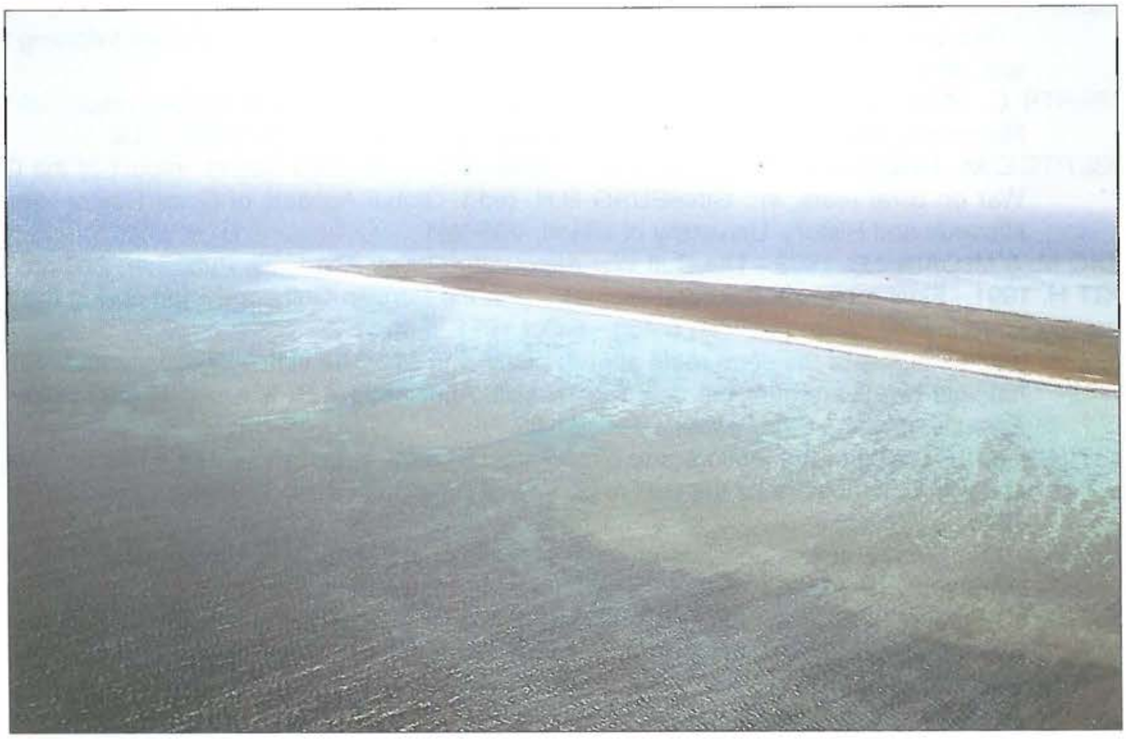

Photo 2: Although the shoreline of Karan Island (Saudi Arabia) was heavily impacted by the Gulf War oil spill, the coral reefs survived remarkably unscathed (Photo F. Krupp).

Photo 3: Although large numbers of *Acropora* were found dead in Kuwait in May 1992, no such observations were made in Saudi Arabia. This *Acropora clathrata* from the fringing reef of Karan Island appears healthy with no signs of tissue degradation (Photo F. Krupp).

A NEW BLEACHING EVENT IN FRENCH POLYNESIA DURING EARLY 1994

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Abstract - In March 1994, the coral reefs of the Society Islands were affected by another important bleaching event. Previous bleaching events were reported in French Polynesia in 1983, 1984, 1987 and 1991. The last one was well recorded and was the most destructive, as about 20% of colonies in the coral community died. It started in early March and ended in September after recovery or death of colonies, which varied by taxa in susceptibility to bleaching and mortality. The most affected genus was *Acropora*. The 1994 bleaching also started in early March and was correlated with a sea surface temperature of 29 to 30°C, 1 to 2°C higher than usual during the hot season. We noted also calm air and seas and low precipitation.

The bleaching event was quantitatively recorded on Moorea, sister island of Tahiti, in the lagoon and on the outer slope of the barrier reef of the Tiahura zone. On the outer slope we noted in April the following prevalence of bleaching (partial or total) of the major genera of reef-forming corals: *Acropora* (which comprises 22% of the colonies in the community) 98%, *Pocillopora* (53% of colonies) 43%, *Montipora* (11% of colonies) 93%, *Porites* (7% of colonies) 6%. On the barrier reef within the lagoon, between 11 and 24% of the coral colonies bleached, prevalence also varying by taxa: *Porites* 10%, *Pocillopora* 89%, *Montipora* 78%. The fate of colonies of two species of *Acropora* that were bleached in April was recorded in July. For *A. latistella*, 67% recovered in totality, 11% died and 22% were partly bleached, dead or healthy. For *A. digitifera*, corresponding numbers were: 38%, 38% and 24%.

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CHANGES IN REEF BENTHOS RELATED TO WATER COLUMN EUTROPHICATION ?

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Abstract - The fringing coral reefs of the Netherlands Antilles show clear gradients in pristine to deteriorated benthic communities. A variety of anthropogenic and natural factors are involved, such as run-off, beach construction, thermal pollution and disease. Except for the impact of white band disease, the effects of these disturbances are rather local, noticeable relatively close to the source. Nevertheless, there are clear indications of larger scale changes along the coasts and in this case the cause of degradation is much more elusive. Such changes appear to be most obvious in the shallower part of the reef ($< = 20$ m) and have been recorded as change in composition/cover of coral communities since 1973.

There are additional long-term data on benthic organisms and recent studies have shown enormous increases in densities of compound ascidians over the last 15 years. Because these organisms are heterotrophic filter feeders, we suspect small changes in water quality, caused by eutrophication of the water column, such as increased bacterial production to be responsible for these subtle large scale changes.

MINERALOGY AND GEOCHEMISTRY OF LAGOONAL SEDIMENTS FROM MAURITIUS: HUMAN IMPACT ON CORAL REEF ECOSYSTEM AT MAURITIUS ISLAND, INDIAN OCEAN.

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Abstract - Mauritius island located in the western Indian Ocean, together with Rodrigues and Réunion islands make up the Mascareignes archipelago. Indications of coral damage were observed in 1987. Subsequently, a pluridisciplinary study of the Mauritian littoral ecosystem was organized by the European Community and later by the Swiss National Foundation of Scientific Research, to determine if lethal pollutions are of human origin.

Mineralogical analyses show that lagoons are characterized by carbonate sedimentation, with aragonite, calcite and magnesian calcite. Mixed with carbonate sediments, detritic sedimentation is present in river outlets with phyllosilicates, quartz, plagioclases, hematite, goethite, gibbsite. The island's soils consist essentially of iron and aluminium oxy-hydroxydes, resulting from ferralitic and bisialitic processes induced by the alkaline volcanic substratum and tropical humid climate.

In comparison, analysis of chemical elements soluble in chlorhydric acid shows that contents of detrital cations (Mn, Fe, Al, K), SiO_2 and PO_4 covary with contents in detrital minerals, and rates of carbonatophilous elements (Ca, Mg, Sr) covary with contents in carbonate minerals.

Coprostanol determinations made in the north of the island show high contents in densely populated areas and in estuaries.

The trace elements Co and Cr seem to be linked to the detritic phase; the other trace elements (Ni, Cu, Zn, Pb, Cd) could be anthropic pollution indicators.

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THE POTENTIAL IMPACTS OF CLIMATE CHANGE ON CORALS AND CORAL REEFS.

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Abstract - The poster describes some of the techniques being used and some of the preliminary results of a project that is currently funded by the Overseas Development Administration of the British Government. The aims of this project are (1) to match potential biological indicators of climate change (ie. bleaching, reef community changes) with detailed on-site environmental information, (2) to evaluate

the effects of changes in ultraviolet radiation (UVR) and photosynthetically active radiation (PAR) on the biology of corals, and (3) to predict the short-term and long-term effects of sea-level rise, increased seawater temperature and increased UVR on coral reefs and their implications for coastal management.

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THE ENVIRONMENTAL IMPACT OF POINT SOURCE POLLUTION ON CORAL REEFS IN HAWAII

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Abstract - Recent declines in the environmental quality of coral reefs particularly near urban centers in many parts of the world, have intensified scientific concern over causal factors. A symposium entitled "Health, Hazards and History of Coral Reefs" held in Miami, Florida in 1993, identified eutrophication, overfishing and sedimentation as the most common widespread sources of stress to coral reefs. In order to assess the current status of coral reefs in Hawaii, a survey and analysis of 23 sites exposed to varying degrees of stress from the above as well as other factors was recently conducted. The results of this study show that eutrophication associated with the discharge of point source sewage effluent produces no measurable negative environmental impact in Hawaii. On the contrary, the data indicate that enhancement to coral reef communities occurs around sewer outfalls particularly with regards to fish populations. The single most negative factor affecting the coral reef communities selected for study was fishing. This accounted for a reduction in fish biomass of 45 g m^2 (wet weight) between stations fished versus stations protected from fishing (Figure 1). Modelling studies using the ECOPATH model, suggest that average Hawaiian coral reefs that are unfished can theoretically support a steady state biomass (wet weight) of 65 g m^2. Hence, impacts associated with fishing are very significant.

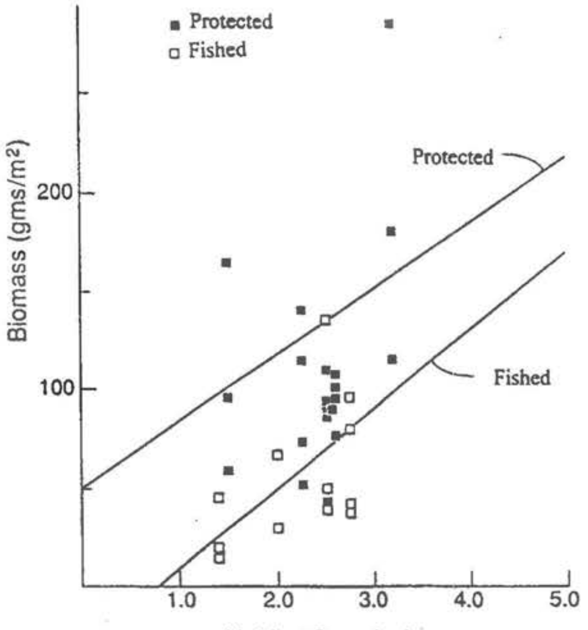

Fig. 1. Regression of fish biomass for stations protected from fishing (top line), and station unprotected (bottom line), against habitat complexity (bottom rugosity, or Relief Index)

CATASTROPHES, PHASE-SHIFTS AND LARGE-SCALE DEGRADATION OF A CARIBBEAN CORAL REEF

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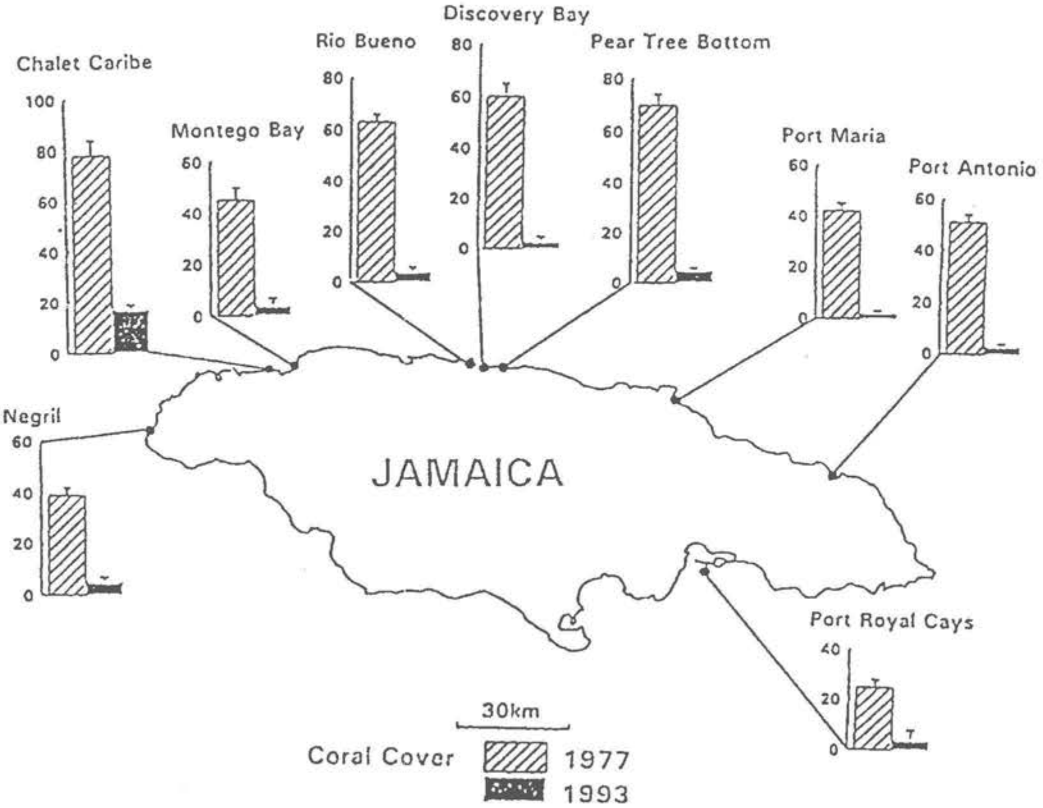
Abstract - Many coral reefs have been degraded over the past two to three decades through a combination of human and natural disturbances. In Jamaica, the effects of overfishing, hurricane damage, and disease have combined to destroy most corals, whose abundance has declined from > 50% in the late 1970's to <5% today. A dramatic phase-shift has occurred, producing a system dominated by fleshy macro-algae (>90% cover). The causes of these changes are complex, and include overfishing, hurricanes, and a continuing algal bloom following disease of echinoid herbivores which began a decade ago. This sequence of events highlights the dynamic and complex nature of coral reefs, points to the fundamental importance of herbivory and recovery from physical disturbance to their functioning, and provides a clear demonstration of how quickly (1-2 decades) a seemingly healthy coral reef can be severely damaged on a spatial scale similar to the size of most tropical island-nations (100's of km). Immediate implementation of management procedures is necessary to avoid further catastrophic damage.



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EFFECTS OF SOLAR INDUCED BLEACHING ON ENDOSYMBIOTIC ZOOXANTHELLAE IN *Goniastrea aspera.*

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Abstract - Colonies of *Goniastrea aspera* from intertidal reef flats at Ko Phuket, Thailand show a particular type of bleaching that is induced during periods of sub-aerial exposure with high sun altitude and irradiance. In the present study we have investigated bleached and non-bleached tissues to determine (1) the distribution and abundance of zooxanthellae in different tissue areas of the host tissue, (2) the histopathological changes occurring in both zooxanthellae and animal cells, and mechanisms of zooxanthella loss, during bleaching, and (3) the effect that bleaching has on zooxanthellae chlorophyll pigments. The results show that zooxanthellae from bleached tissues degrade within their host cell vacuole leading to a reduction in numbers of zooxanthellae from all tissue areas, apart from basal tissues. Host cells containing degraded zooxanthellae showed signs of damage themselves, whereas no other animal cells showed signs of damage. Chlorophyll a concentrations did not vary significantly between bleached and non-bleached tissues, however, there was significantly lower chlorophyll *c* concentrations in zooxanthellae from bleached tissues.

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SIX YEARS OF CHANGE IN A STRESSED PHILIPPINE REEF FISH COMMUNITY

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Abstract - An analysis of six-years of alternate-monthly visual transect data from Bolinao (Western Luzon) indicated that 10-20 dominant species recruited annually in April-May to the reef slope. Daytime visual and nocturnal seagrass trawl transects indicated that recruitment to the reef flat was less predictable and sometimes bimodal. Fishing pressure in both the reef slope and flat was intense (about 3 times higher on the reef flat, but reasonably constant throughout the study period. The reef slope fish community underwent a distinct shift in mid-1988, possibly related to a decline in coral cover from approximately 30% to 15%, as indicated by other studies. This is supported by the shift from more-coral preferential to less-coral preferential fish species ($p = 0.5$, sign test on significantly changing species). Fish abundances on the reef flat seagrass beds declined by about 20% ($r = -0.48$), and showed no significant change in species per transect, but an increase in H' ($r = 0.64$). This was due to a sharp increase in evenness ($r = 0.86$), thus possibly indicating that fishing stress does not necessarily cause a decline in diversity as commonly measured. Abundances of adult fish remained fairly constant. A novel test of dynamic trend (COSMA) indicated that this community was strongly cyclic annually ($p = 0.01$), but accelerating in its rate of change ($p = 0.02$), indicating increasing instability. Analyses of the reef slope data over time and in cumulative transects for all stages of fish in a non-recruitment month (January l993) and for juveniles in a recruitment month (May 1993) indicate a predictable relationship in the number of species (S) versus number of individuals (N) (S =

$2.24N^{1/2}$, r = 0.87, 0.96, 0.96 respectively in linearized form). This supports early conjectures by Peter Sale from a global perspective, and raises the possibility that in the absence of effective reserves, widespread intensive fishing on reefs could threaten the maintenance of natural levels of fish species diversity.

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CORAL REEF DECLINE IN THE CARIBBEAN REGION

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Abstract - There is increasing concern with the widely reported decline in coral reefs in the Caribbean region. For example, 8 of 14 sites in the CARICOMP (Caribbean Coastal Marine Productivity) network of marine laboratories, parks, and reserves indicated that coral cover had declined over the past 10 years. Other Caribbean sites reported declines at the June 1993 meeting in Miami on global reef status. The most common manifestation of decline at all sites is decrease in coral cover and an increase in benthic algal cover.

It is instructive to re-examine the region-wide mass mortality of the herbivorous sea urchin *Diadema antillarum* in 1983-84 which is highlighted at all sites as a critical event. Little noticed even decades ago by their first scientific visitors, who pronounced them undisturbed, many Caribbean reefs may have been teetering on the edge of dramatic anthropogenic change from the subtle, early impact of over-fishing of large predacious and herbivorous fishes. *Diadema* populations, released from predation, attained unprecedented, high population densities, compensating for the loss of herbivorous fishes, and controlling benthic algae. The mass mortality removed this remaining herbivore and the balance of coral and algae dramatically shifted to an alternate state of algal dominance. The mass mortality acted in synergy with a number of circumstances which lowered thresholds for macro-algal dominance over corals including increased availability of nutrients, increased sedimentation associated with deforestation, storm damage, bleaching, disease, and other human-induced stresses.

Another impact of over-fishing is the release from predation of damselfishes which kill coral to create algal patches which they maintain. The superabundance of damselfishes virtually assures that any new coral recruit will be discovered and killed before it can attain sufficient size to escape. Importantly, 6 of 14 CARICOMP sites reporting no recent loss in coral cover are located within parks or reserves where controlled fishing access is the only management tactic.

Reefs, with widely dispersed meta-populations and a low, steady supply of inorganic nutrients, are resilient to periodic natural disturbance which plays a major role in the maintenance of reef biological diversity. Chronic human disturbance, often beginning with and sustained by relentless over-fishing, exaggerates the impact of natural disturbances and reefs may shift to alternative states.

Survival and recovery of reefs accessible to large human populations may depend on strict fishing regulations as a critical first step in management. Protection of more remote reefs will require inter-governmental cooperation in survey, monitoring, comparative research, and integrated coastal management within global sub-regions, such as the tropical western Atlantic, encompassing the geographic range of reef meta-populations and of key ocean processes.

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CO_2 RISE AND CORAL REEF BLEACHING

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Abstract - Supported by theoretical arguments and preliminary physiological experiments, we think that CO_2 rise is the cause of the recent, worldwide and massive bleaching of photosynthetic symbioses in coral reefs.

"Bleaching" is the common name for the rupture of the symbiotic relation, and affects the founder of the reef ecosystems: corals and other cnidarians, *Tridacna* molluscs, larger foraminifera and sponges in association with either dinoflagellates, diatoms or cyanobacteria. Appeared in the last decade, massive bleaching is increasing in magnitude and becoming chronic. It is worlwide, observed in all reef biotopes, in polluted as well as pristine areas, in isolated islands to barrier reefs, from lagoon to fore-reef, from surface down to 100 m depth, without coherent spatial pattern, except may be with passes and groove structures. It happens generally during summer, often when calm weather and clear sky. Mortality is very variable, ranging from total recovery to death up to 97%.

The most worrisome is that the global environmental cause of mass bleaching is unidentified. Global warming has been often invoked, but is undetected at regional and local scales, and there are good counter-examples. UV increase due to ozone loss, sometime considered, must be excluded as no UV change is yet measured in the tropical zone. A hypothetical global change of weather pattern and hydrology appears incompatible with the variety of affected microenvironments.

CO_2 rise might be well the additional stress throwing reef photosymbioses out of equilibrium when they are subjected to yearly maximum temperature and light. The 30% rise of CO_2 since pre-industrial time is the most pervasive global change affecting ocean shallow waters. It has induced an acidification of the otherwise fairly well buffered seawater of almost 0.1 pH unit. For geochemist, CO_2 is a control of reef biocalcification at the global level.

The bleaching phenomenon is not understood at the biological level, but, as it affects all and quasi-exclusively photosynthetic symbioses, it implies the perturbation of a basic biochemical process of host/symbiont exchange related to photosynthesis. A very important one is the bicarbonate pumping by the host (probably controlled by cytoplasmic pH) to provide enough CO_2 to the symbionts. It is indicated for example by the heavy organic δ^{13}Carbon, with interspecific values following closely bleaching sensibility. Corals and larger foraminifera (at least) are also quite exceptional as the increase of CO_2 reduces their photosynthesis, contrary to all other phototrophs.

We conducted an experiment which indicates that CO_2 is an important factor of bleaching, at least in synergy with high temperature and light. Tips of the coral *Stylophora pistillata* were subjected to summer conditions (raises of temperature from 22.5 to 24°C and light from 75 to 550 μE/m2.s) under three levels of CO_2: normal 360ppm, ~l000ppm and ~5000ppm CO_2 for two days before transfer back to normal conditions. Corals in the control aquarium appeared always healthy. At l000ppm CO_2, there was strong reduction of photosynthesis, and visible paling and closure of polyps for two weeks. In the high pCO_2 condition, the tips showed the first sign of bleaching after 24 hours, then were bleached after 40 hours, and died all within 2 weeks.

If CO_2 rise is the weak additional stress responsible of bleaching, it will have deep implications.

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WHAT HAPPENED TO REEF ECOSYSTEMS DURING THE TRIASSIC-JURASSIC INTERVAL ?

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Abstract - Reef activities were concentrated along the extensive shallow-water shelves that characterized the equitable warm-water Tethys seaway during Late Triassic time. Here bordering Pangea, corals, sponges, spongiomorphs, calcareous algae, foraminifers, a variety of problematic organisms and other shelly invertebrates developed complex paleoecologic relationships in diverse reef settings. Here zooxanthellate scleractinian corals evolved and diversified. By latest Triassic time they had become important constructional elements coexisting with secondary framework builders-chambered sponges and spongiomorphs.

During a mass extinction event some 200+ ma. at the end of the Triassic, this flourishing Tethys ecosystem collapsed rather abruptly and carbonate sedimentation nearly ceased. While the cause(s) of this mass extinction continue to be discussed and debated, the devastating effects, as measured by loss of taxonomic diversity and community structure, seem clearly apparent. In a pattern reiterative for Phanerozoic reef history, the end-Triassic reef collapse was followed by a Jurassic perturbation interval and reefbuilding was disrupted on a global scale for 4-10 ma. In the Tethys reefbuilding was lost entirely. During the Hettangian-Sinemurian stages of the Early Jurassic in the Tethys only some scattered non-reef fossil localities are known. In other areas of the Tethys deep-water(?) mud mounds are known but framework is absent.

Outside the Tethys during Late Triassic time, reef communities similar to those of the Tethys also existed at tropical to subtropical latitudes but compared with those of the Tethys, the fossil records are exceedingly poor and knowledge is proportionally much less. Most reefs developed as clusters of volcanic islands or island chains within the ancient Pacific and more or less comparable to those of the present-day Pacific. Unfortunately, the dynamics of sea floor spreading and subduction have swept the seafloor clean, destroying most evidence except where remnants of these reefs occur in the circum-Pacific terrane collage. The Late Triassic volcanic reefs have been found in the Cordilleran terrane collage of North America compare somewhat with Tethyan counterparts but most examples present different morphologies, facies relationships, ecologic structures and biotic composition suggesting different origins and a degree of isolation from the Tethys.

Paleoecological and stratigraphical studies of these Triassic volcanic reefs in western North America resulted in the discovery of Lazarus taxa with Paleozoic holdover sponges and algae. They provide important evidence for a neglected part of the evolutionary history of reefs in regions far-removed from the Tethys. Discovery of the first Early Jurassic coral reef in the volcanic terrane of Stikinia in British Columbia, Canada, reveals that reefbuilding actually continued during the perturbation interval between Triassic and Jurassic time. The principal reefbuilding coral on this Early Jurassic reef was a Late Triassic Tethyan species previously thought extinct. Such scattered reefs provide evidence that volcanic islands of the ancient Pacific functioned as refuges allowing preferential survival of some reef taxa and the continuation of reef evolution during the critical post-extinction interval. The refuge idea may apply also to other Phanerozoic mass extinction events where similar biotic patterns are indicated. The implications of the refuge idea are significant in understanding evolutionary dynamics and biotic turnover.

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REEF DEGRADATION AND EVOLUTION AROUND THE TIME OF THE CRETACEOUS/TERTIARY BOUNDARY ON A TETHYAN CARBONATE PLATFORM (MONTAGNA DELLA MAIELLA, ITALY)

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Abstract - Upper Cretaceous and Palaeogene reef limestones from the Maiella carbonate platform allow the investigation of how reefs evolved in the Mediterranean Tethys during a time of faunal turnover.

Shortly before the Cretaceous/Tertiary boundary, rudists, that build a thick series of platform carbonates with biostromes, died out on the Maiella platform. Several lineages of other organisms, particularly of larger foraminifera, also disappeared at this time.

Coral-algal-dominated reefs represent a new type of sedimentation that was established on the Maiella platform at latest by the Late Danian-Early Thanetian. The evolution of this reef type is characterized by long-term changes, supposedly gradual, as the builder and binder guilds of reef organisms, scleractinians and red algae in the first place, radiated. Another remarkable taxonomic change is the first appearance of new lineages of larger foraminifera in the Thanetian. The Paleocene reef sediments are preserved as slide blocks and as boulders redeposited onto the platform slope during the course of the Paleocene.

The Late Cretaceous and Paleocene evolution of the Maiella carbonate platform, its shallow-water communities, and the types of reefs they built, were strongly influenced by repeated fluctuations of the relative sea-level. These sea-level changes may have been eustatically influenced, as large fluctuations of sea-level were recorded from other regions during the Late Cretaceous and the Paleocene. Climate appears to have been generally warm during this period, although the influences of short-term climatic deterioration and other environmental controls, such as ocean chemistry, are as yet unclear.

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STATUS OF THE CORAL REEFS - BEFORE AND AFTER THE GULF WAR

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Abstract - In comparison to other coral reef regions, the corals in the Persian/Arabian Gulf exist in extreme living conditions and strong seasonal variations. The water temperature normally varies between 15 - 33°C. However, during the winter, temperatures may fall to as low as 10°C and may reach 40°C during summer. In the winter 1988/89, low water temperatures led to the death of large numbers of *Acropora pharaonis* and *Platygyra daedalea* in some reefs in Saudi Arabia. High evaporation rates, limited water exchange through the Strait of Hormuz and low freshwater input cause high salinities in the Gulf. The combined effects of extreme temperature, high salinities, as well as high turbidity in coastal areas limit the number of Scleractinia genera to only 30. In comparison, 138

Scleractinia genera occur in the Indo-Pacific. In addition to these factors, coral reefs are also subject to human impact. This includes the numerous coastal construction works, dredging of channels, and in particular the activities of the oil industry.

However, in January 1991 the largest ever recorded amount of oil was released deliberately at the end of the Gulf War. Although estimations vary widely, approximately 4-6 m barrels of oil were spilled into the marine environment. This amount of oil did not only pose a threat to the Kuwaiti coral reefs, but because the currents transported the oil southwards, it also endangered the Saudi Arabian reefs, which are known to be comparatively rich in species composition

However, this study, as well as the findings of other workers failed to detect any damage to the Saudi Arabian reefs. Oil or tar was not found in the reefs and abnormally large numbers of bleached or dead corals were not observed. The live coral cover remained stable at the 10 study sites during the investigation period of June 1992 to July 1993.

These findings differ from investigations conducted in Kuwaiti reefs. Although no signs of impact were visible in September 1991, other researchers detected large numbers of bleached and dead corals in spring 1992. However, consequent investigation of the damaged reefs concluded that the initial reports had overestimated the impact and that recovery was well underway. A link between the oil spill and the documented reef impact could not be proved. It may be that natural, as well as man made factors caused the damage. More recent studies in the southern parts of the Gulf not reached by the oil spill, show the bleaching and death of corals on a large scale. These findings have been attributed to low tides with subsequent exposure to low air temperatures.

In summary, although the largest ever recorded oil spill drifted over many coral reefs, the oil has had limited, if any effect on the corals so far.

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REEF MONITORING AND MANAGEMENT

CORAL DISEASES AS INDICATORS OF REEF HEALTH : FIELD METHODS

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Abstract - A semi-quantitative and a quantitative method have been used to assess the health condition of coral reefs. Both require the ability to recognize coral diseases *in situ* under water. The semi-quantitative Belt Method is a time-count technique that uses 30-minute scans to quantify frequency of occurrence of coral diseases on a scale from zero to six.

The quantitative Point Method is a plotless line-transect technique that records evenly spaced points of coral surface. In the case of afflicted corals, the disease is registered even if the transect point touches a healthy part of the coral specimen. Special modifications of the line-transect approach can either enormously increase the plotless data base, or convert the technique into a genuine sample-plot method.

1. INTRODUCTION

What reef health really is will probably always remain a matter of debate. The lively workshop on Reef Degradation, held at the ISRS meeting, September 1994 in Luxembourg, was a case in point. There are, of course, many ways to describe, define, or quantify the "health" or "vitality" of coral reefs, as exemplified by one of the latest overviews on this subject (GINSBURG 1993). To review and discuss the present state of the art of this field, however, is not the aim of this paper. It merely attempts to describe some new tools of reef assessment that can be added to the array already in use.

Thus, one possible, perhaps supplemental, approach to the question is to use coral diseases as indicators of reef health (ANTONIUS 1987a). A review of these diseases and pathologic syndromes is given in ANTONIUS (1995), while other coral-destroying agents are listed in ANTONIUS (1993).

The methods under consideration here are fast and easy-to-apply semi-quantitative techniques (*e.g.* ANTONIUS 1988a), as well as quantitative methods (*e.g.* ANTONIUS & WEINER 1982). They can all be carried out either snorkeling or SCUBA diving, depending on reef morphology and the depth-zonations surveyed.

2. THE BELT METHOD

The Belt Method is a semi-quantitative time-count technique that developed out of routine checks on reef health. Essentially it is a derivative of visual census techniques that were developed to count reef fishes (*e.g.* BROCK 1954; ANTONIUS *et al.* 1978; RUSSELL *et al.* 1978) and to assess *Acanthaster* infestations (*e.g.* ANTONIUS 1971; ENDEAN 1974). Surveying a coral reef, it is relatively easy to note down all cases of active diseases on corals that are encountered. Making this approach semi-quantitative merely requires standardisation :

1) a time-frame limiting the duration of each individual survey-swim, and
2) organising the number of every disease encountered into categories.

The time-frame of one single survey-swim is half-an-hour. During this period, the diver swims fairly close to the reef surface and registers all pathologic syndromes on corals in a path, or "belt", about 2m wide. One such 30 minute survey is considered a "scan". The diver's speed during such a scan may vary. In scarcely populated reef areas and/or reef zones with large coral colonies, the diver will proceed faster and cover more distance than in densely populated reef areas and/or reef zones with smaller coral colonies. However, experience has shown that the total number of coral colonies investigated during one scan remains surprisingly constant (*e.g.* ANTONIUS 1988a). In order to assure this consistency, the time-count has to be interrupted every time the diver traverses completely barren reef areas.

The categories for the instances of diseases encountered range from zero to six. Zero (0) naturally means no syndrome found. A disease is considered condition (1) "rare", when 1-3 cases are found during a 30 minute scan; condition (2) "moderate", stands for 4-12 cases; (3) "frequent", represents 13-25 cases (ANTONIUS 1987b; 1988b); (4) "abundant", means 26-50 cases (ANTONIUS 1988a); (5) "epidemic", is used when 51-100 cases are found; and (6) "catastrophic", is the end of the scale, when the number of syndromes exceeds 100, which means that the number of diseases actually becomes uncountable (ANTONIUS 1991). The particular numerical values of these six categories have been determined as the most useful based on practical experience during many years of fieldwork. They are not derived from statistical theory.

The method, in it's above form, neglects the portion of completely dead corals. Thus, if desired, an account of dead versus living reef has to be given separately. On the other hand, impacts on corals other than genuine diseases can be listed, such as coral-overgrowing algae (*e.g. Lobophora variegata*), sponges (*e.g. Terpios hoshinota*), zoanthids (*e.g. Palythoa* sp.), or ascidians (*e.g.* Didemnidae), as well as cases of outright predation, such as polychaetes (*e.g. Hermodice carunculata*), snails (*e.g. Turbo, Drupella, Cyphoma* species), or seastars (*Acanthaster planci*).

Since the Belt Method is fast and simple to use - requiring only a watch, a writing slate, and a pencil - it is very well suited to survey large reef tracts. Under reasonably calm conditions, kilometres of linear reef extension can be surveyed during one day. In fact, using the Belt Method, it is easy to acquire a sample size large enough to average out any possible bias of the observer, irregularities of the survey site, or both. The emerging data soon reveal where problem zones may be located in a reef system. These areas can then be picked out and scrutinised by quantitative means.

3. THE POINT METHOD

Compared to other quantitative reef assessment methods, such as the Intersected Length Method, the Quarter Point Method, or the Belt Quadrat Method (DODGE *et al.* 1982), the Point Method is relatively fast and simple to use. The basic tool is a transect line, usually 100m long, that is strung out over a reef. The line is marked at evenly spaced intervals, at which points the underlying substrate is recorded : this can be different types of inorganic substrate, such as sand, rubble, or rock, and it can be any kind of sessile organism such as alga, seagrass, sponge, soft coral, horny coral, stony coral, etc. In contrast to other line transect methods (*e.g.* LOYA 1978), these organisms are never measured, only the point of contact is recorded. However, in order to obtain the additional information on reef health, the technique is modified somewhat. If a transect point touches a coral colony that is afflicted with some kind of pathologic syndrome, not only the coral species is registered, but also the disease - even if the diseased area is not exactly below the transect point.

As in the case with the Belt Method, the Point Method can also record other types of coral destroying agents such as coral overgrowing organisms, coral predators, up to human-related (even military!) disturbance (ANTONIUS & WEINER 1982). In short, any kind of impact on reef corals can be registered.

The accuracy of the resulting quantitative read-out on reef health can be tailored to need. For a rapid large-scale survey, for instance, transect points can be spaced at 1m intervals (ANTONIUS 1974; ANTONIUS & WEINER 1982), for more detailed studies at 0.5m (ANTONIUS 1980a; ANTONIUS *et al.* 1978; DODGE *et al.* 1982), and for very accurate, smaller-scale surveys even at 25cm intervals, in which case a transect line of 50m or less is used (ANTONIUS 1980b).

4. TRANSECT MODIFICATIONS

If enough time is available for such a reef health assessment, modifications of the Point Method are possible which take advantage of the transect line that has already been laid out over the reef. Either the plotless data base can be increased manifold, or the technique can be converted into a plot method.

The additional tool is an aluminium meter-stick, which is moved along perpendicular to the transect line. In order to augment the plotless data base, the meter-stick is laid down at every line-transect point and additional point recordings are made at certain intervals along the stick, usually at 20, 25, or 33cm. This can be done on both sides of the transect line, making this technique a simple extension of the Point Method (ANTONIUS *et al.* 1989).

But it can also be converted into a quantitative plot method by recording a 1m-wide belt on each side of the transect line. The stick is continuously moved along perpendicular to the transect line, as slowly as necessary, and every coral colony it passes is inspected for pathologic syndromes. A continuous belt, though, is rarely the form in which data are desired. A much better understanding of reef zonation is obtained when the belt is broken down into sub-units. Thus, data can be lumped for $1m^2$, $2m^2$, or even $5m^2$ units (ANTONIUS 1984). Also, the plot units do not have to be consecutive, but can themselves be spaced at certain intervals (*e.g.* 5m, 10m, etc.) along the transect line (STODDART 1969; 1972). If working time permits and all corals, not only the diseased ones can be recorded, information is generated not only on reef health, but also on species composition, frequency of occurrence, and diversity. An account of the statistical processing of data generated by the Point Method and other methods is given in DODGE *et al.* (1982).

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SUSTAINABLE MANAGEMENT OF THE COASTAL AREA OF SW SULAWESI

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Abstract - What are the effects of the bio-physical, social-economical and social- cultural factors on the sustainability of the coastal ecosystems in SW Sulawesi as natural resources ?

The aim of this program is to enhance scientific knowledge directly related to the preservation of coastal ecosystems of SW Sulawesi. These ecosystems are adversely affected by human interference processus that are rooted in the local economy and social structure. The emphasis of the program is on the sustainable use of coastal resources taking into account the direct impact of both human activities and (bio)physical processus.

The research will be conducted by a multidisciplinary group of scientists from various institutions in the Netherlands, in cooperation with Indonesian counterparts from 1994 - 1998. This interdisciplinary program will be embedded in the framework of the Buginesia Program, a cooperation existing since 1980 in marine sciences between Dutch researchers and the Hasanuddin University in Ujung Pandang, which has been appointed as the main Indonesian University for marine sciences and coastal management. This long-standing cooperation has the advantage of an existing logistic infrastructure and an extensive scientific database of the coastal area of SW Sulawesi.

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EVALUATION OF REEF HEALTH AT THE COMMUNITY, ORGANISM AND MOLECULAR LEVELS

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Abstract - An ability to evaluate reef health or condition is likely to become an increasingly important goal for many reef scientists during the next decade. This paper provides an overview of the sensitivity of community, organism and molecular approaches in establishing the condition of corals and coral reefs. Lethal effects, for example, are indicated by benthic community change and provide a retrospective view of damage done. Physiological, biochemical and cellular indices of stress may offer forewarning of incipient deleterious effects. Such indices are extensively used in temperate waters but have been rarely tested on coral reefs. At the coral colony level the indices include measurements of growth, metabolism, scope of regeneration of lesions, susceptibility to disease, zooxanthellae density and division rates, chlorophyll concentrations, enzyme and protein determinations as well as the synthesis of 'stress' proteins. Using established case-histories the advantages and limitations of available methodologies will be discussed and the conclusions will form an introduction to the proposed workshop on assessment of reef health.

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INTEGRATION OF ENVIRONMENTAL, SOCIAL AND ECONOMIC ISSUES IN EVALUATION OF CORAL REEF USAGE OPTIONS

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Abstract - Coral reefs are amongst the most diverse and productive ecosystems in existence and are suffering degradation the world over. One factor contributing to the degradation is that economic methods used to evaluate projects tend to underestimate the worth of natural resources. Economic methods often assess value on some dimensions poorly and ignore other dimensions altogether. Conversely, multiple criteria techniques are designed to accommodate the multiple dimensions of conflicting management objectives. The goal of this research is to provide decision-makers with a more comprehensive framework for information evaluation. This will enable more informed judgements regarding the ecological sustainability and social acceptability of coral reef usage options.

Specifically, this work will compare the relative utility, and validity, of an economic and a multiple criteria evaluation of a coral reef management decision. The case study chosen is the decision regarding the future functioning of Saba Marine Park. This Park surrounds the island of Saba, one of the Netherlands Antilles in the Caribbean.

To date, the framework for analysis, the multiple criteria technique and the data sampling tools have been chosen based on the characteristics of the project being assessed. Such characteristics include the amount and quality of the data available, the degree of participation of users and decision-makers in the analysis and the size of the project. Social, environmental, political and economic objectives will be incorporated in the analysis. The development of the multiple criteria framework for analysis will be discussed and preliminary data will be presented.

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REEFBASE: PRIORITIZING GLOBAL INFORMATION NEEDS

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Abstract - During the 1993 meeting, Global Aspects of Coral Reefs, many scientists presented evidence that various coral reefs around the world were in a state of decline. Although it is now clear that there is a global problem, it is not possible to determine how great the problem is. Similarly, it is not possible to make a reliable estimate of how much fishery production comes from coral reefs, how much production should come from reefs, how much reef area exists in the world, or even what the

average coral reef looks like, in terms of geomorphology and bottom cover. Perhaps most distressingly, it is not possible to determine what is and is not a healthy reef, because the "norm" for what a "normal" reef of any particular type should look like has never been established.

ReefBase is a global coral reef database which is being developed to address concerns such as these. The basic idea is to develop a primarily quantitative database, similar to ICLARM's FishBase, which would summarize information on reef production, health, threats, etc. in a form for easy retrieval and summarization. Data will be obtained from papers and reports, and credit given in all cases to the original sources. All sources will be maintained and made available through the ICLARM library.

The project design was based on a workshop in Australia in 1992, and revised following an initiation workshop in the U.K. in January, 1994. Currently, the initial tables of the database are being finalized in draft form at ICLARM. Reef mapping and area quantification are being carried out at the World Conservation Monitoring Center (WCMC) in Cambridge, U.K. The project aims at releasing the database and other linked databases on CD-ROM by the 1996 International Coral Reef Symposium. A second, expanded version should be available two years later.

The present workshop will be aimed at making adjustments to the content and focus of the database. We are seeking positive suggestions as to how the database can be improved so as to be optimally beneficial to coral reef scientists, particularly those in developing countries.
For copies of the draft database forms, please contact:

Project ReefBase, ICLARM
MCC P.O. Box 2631, 0718
Makati, Metro Manila, Philippines
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REGENERATION OF TISSUE LESIONS IN CORALS : A BIOMONITORING TOOL ?

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Abstract - Regeneration of tissue damage in corals has been described since the beginning of the century, but quantitative data have only been available since the mid seventies. To date research has been done on various aspects of scleractinian regeneration including species variation in regeneration rates, effects of sedimentation and bleaching, effects of lesion morphology, and the influence of regeneration on growth and reproduction. Results prove that regeneration is a vital and sensitive process in coral ecology. However, not all species are equally affected under similar environmental conditions, and selection of one or more indicator species is a requisite for successful monitoring. In the Caribbean sensitive and fitting species appear to be the most important reef-building species.

The use of growth and reproduction as biomonitoring tool has been suggested as they are known to be affected by environmental changes. Both are suppressed by regeneration and this suggests that monitoring regeneration could be a valuable tool to investigate coral health. Moreover, the proposed method has great advantages over monitoring growth and reproduction. The method is inexpensive, easy to use, non-destructive and fast. Results can be obtained in less than 2 weeks.

Since most of the world's reefs are in developing countries where logistics and technological supplies are always limited, an effective tool should be both cheap and easy to use.

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CORAL BREAKAGE ON REEFS - A PROBLEM FOR MANAGEMENT ?

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Abstract - The amount of coral breakage, the taxa most frequently affected, and management implications were investigated on various reefs in North Africa (Egyptian Red Sea) and South Africa (Maputoland Reef Complexes) which are subject to human pressure by fishing, boating, and recreational diving.

In North Africa, breakage was the most frequent of four investigated damage types (minor and major tissue loss, algal overgrowth, breakage). Especially *Millepora dichotoma* and *Acropora* were affected. Most damage was done in shallow areas - on reef flats, reef edges, and the tops of patch reefs by careless anchoring, but also by diving activities. Damage was localised and serious on some reefs, but overall did not appear to threaten coral communities.

In South Africa, breakage occurred mainly in deeper areas (18-24m) dominated by branching corals (*Acropora florida*). Up to 100% of all branching colonies had been broken at some stage. This could not be only attributed to human activities, but also to recurrent heavy storm swells. Numerous colonies appeared to have recruited from fragments. Experiments proved that in shallow water fragments had no survival chances. In deep water, only big fragments survived. Small cylindrical fragments, as usually produced by divers, exhibited 93% mortality within the first month.

This study indicates that depending on the area and the extent of coral breakage, serious community degradation can take place. While in North Africa localised breakage had no detectable influence on coral community composition, in South Africa, however, breakage of *Acropora* could lead to their total disappearance from shallow reef parts.

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DEVELOPMENT OF AN ECOTOXICOLOGY APPROACH FOR USE IN ASSESSING "HEALTH" OF REEFS

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Abstract - One approach to monitoring the "health" of reefs is to monitor the "health" of the corals themselves. Good "health" is as difficult to define in corals as it is in Man. Changes in physiological "health" associated with changes in water quality, could be one indicator. As a first step it is neces-

sary to determine the most useful physiological parameters for this purpose and to find out how they respond to environmental changes.

We have selected measurements of respiration rate (indicative of overall rates of energy expenditure) gross photosynthesis (indicative of overall primary productivity) and skeletal growth rate (indicative of overall rate of reef accretion) for this purpose. This paper will describe preliminary work carried out on *Porites porites* at the Bellairs Research Institute, Barbados, to test the effect of reduced light and reduced temperatures on coral nubbins cultivated under artificial lighting in the laboratory.

After 3 weeks, those maintained under reduced light of 120 $\mu E/m^2/s$ showed typical photoadaptation responses, with increase in both α and Pgross max in the P v I curve in comparison with controls maintained at 400 $\mu E/m^2/s$ and a temperature of 28°C. Those kept at the same irradiance as the control group but a temperature of 23.5°C had a much reduced Pgross max, largely as a result of loss of zooxanthellae. Growth rate was lower in the groups kept at low light and low temperatures than in the control group.

These results gave us confidence in the methodology as a potential tool for use in ecotoxicology studies, and work is now underway in Barbados (by Francesca Marubini) to assess the effects of individual eutrophication components.

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AN INVESTIGATION INTO THE USE OF LESIONS ON CORALS AS INDICATORS OF ENVIRONMENTAL POLLUTION

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Abstract - A number of shallow water sites within 4 locations at St. Croix, US Virgin Islands, were surveyed for coral tissue abnormalities and blemishes. The same sites were also surveyed for traditional measures of community well being: coral cover; species richness; diversity (Shannon's H') and evenness (Pielou's J').

The 4 locations were chosen to represent different levels of environmental pollution, ranging from Buck Island National Park (virtually "pristine") to Christiansted Harbour (adjacent to a medium-sized town, with sewage, power station and desalination plant discharges into the harbour).

No significant pattern was detectable in any of the traditional measures of reef "health" when sites were grouped by location, but significant patterns emerge when sites are grouped by reef-type or ordered by depth (higher species richness and diversity at coral pavement and front fore-reef sites, and increasing species richness and diversity with depth). Using the traditional measures to compare between sites at different levels of pollution is likely to be complicated by differences in, among other things, depth, substrate and wave energy between sites as well as natural patchiness. Those measures may therefore more appropriately be used to record temporal changes on established permanent transects rather than to attempt to quantify reef "health".

The incidence of lesions on corals did vary distinctly and significantly between locations, with the highest incidence of most categories of lesion at Christiansted Harbour and the lowest at Buck Island. Grouping sites by reef-type produced very much weaker patterns.

Analysis of within-species incidence of lesions at different locations revealed that coral species vary in frequency with which they are affected by lesions and in the extent to which the incidence of lesions reflects the levels of pollution, with *Porites astreoides* varying strongly between locations, but *Diploria strigosa* and *Diploria clivosa* showing much less variation.

The species composition and size distribution of corals sampled for lesions varied between locations but was not responsible for the overall pattern of a larger number of lesions at the more polluted locations.

Surveying lesions is therefore a promising means of monitoring environmental pollution, especially as : (1) lesions do not necessarily represent the death of the coral; (2) production of lesions is likely a generalised stress response; and (3) lesion damage is amenable to quantitative measurement.

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ZOOXANTHELLAE MITOTIC INDEX AS AN INDICATOR OF STRESS IN TROPICAL ANEMONE, *Heteractis malu*

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Abstract - Bioassays have been extensively used in temperate marine ecotoxicology in recent years, but there has been relatively little development of such tools for detecting pollution in tropical waters especially using tropical sea anemones and corals. These animals could be good indicators of environmental change in tropical waters, because of their overall abundance, availability throughout the year, their sensitivity to environmental factors and their sedentary nature. Another attractive feature of using these animals in bioassays is the unique relationship between the host animals and their endosymbiotic algae (zooxanthellae), disruption of which has proved to be very sensitive to environmental disturbance.

The division rate of zooxanthellae (expressed as mitotic index) is one of the quantitative parameters which has been used to evaluate responses of the host and its symbiotic algae to pollutants as well as natural environmental factors such as increased temperature and irradiance in the present study.

In the bioassay experiment described here, the tropical anemone, *Heteractis malu* was exposed to three different copper concentrations, 0.01 mgl^{-l} Cu, 0.05 mgl^{-1} Cu and 0.1 mg1^{-1} Cu over a 48 hour period. In control anemones (with no copper addition) division of zooxanthellae was synchronous with peak mitotic index (7.2%) at midday. In copper treatments at concentration of 0.05 mgl^{-l} Cu and 0.1 mgl^{-l} Cu the synchronous nature of zooxanthellae division was completely lost. At the lowest concentration of 0.01 mgl^{-l} Cu synchronous division of zooxanthellae was retained over the first 24 hour period of exposure but was less evident during the subsequent 24 hour period. Significant elevations of mitotic index of zooxanthellae were noted only in anemones exposed to the highest concentration of copper (0.1 mgl^{-l} Cu) after 30 hour when the anemones appeared partly bleached.

Disturbance of the synchronous pattern of zooxanthellae division in some corals and anemones, together with marked elevations in mitotic index of zooxanthellae, may provide an early warning of environmental stress, and may also offer some potential for development as a bioassay tool.

VOLUNTEERS PROGRAMMES IN APPLIED MARINE RESEARCH AND REEF MANAGEMENT

REEF CARE'S CORAL RESEARCH PROGRAMS FOR VOLUNTEERS ON CURAÇAO

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Abstract - Reef Care Curaçao, is a volunteer pool of mostly local sport divers who contribute to coral reef conservation by executing educational, conservation, public awareness and research programs. Two major coral reef research programs are presently underway: a study on annual coral spawning events and a continuous monitoring program on the distribution and abundance of an encrusting and coral killing ascidian. Coral spawning observations started in 1991 involving 75 volunteers and is continued annually. During a one evening workshop, participants receive instructions on potential spawning times of different species and the kind of data that can be collected. This information is made available in a special flyer and spawning observations can also be reported to the Reef Care Alarm Phone. To study the distribution and abundance of the encrusting ascidian *Trididemnum solidum* (VAN NAME), a briefing was compiled and presented to participants at a 6-hour workshop. A total of 42 localities, examined for abundance of the ascidian using a transect method in 1978, were reexamined in 1993 using the same method with the help of volunteers. Permanent quadrats will be placed in several localities and monitored every 6 months. All 42 localities will be revisited in the year 2006. Presently, only local volunteers participate in Reef Care programs. The programs were chosen and adjust for the type of volunteers for which social involvernent and contact with local scientists is very important.

1. INTRODUCTION

Logistic limitations while studying pre-zygotic isolation mechanisms in the polymorphic Caribbean reef building coral *Montastrea annularis* (ELLIS & SOLANDER) (VAN VEGHEL 1994) gave reason to use local sport divers to monitor the reef. A total of 75 divers successfully participated in the project, '1991 Coral Spawning Event', during which spawning data was collected on different reef organisms (VAN VEGHEL 1993b; 1994). The success of this project, in terms of producing useful scientific information and in the enthusiasm of the local divers, resulted in the formation of the organisation 'Reef Care Curaçao,' in December 1992.

Reef Care carries out research projects, *e.g.* studies of coral spawning (VAN VEGHEL 1993b), the distribution and abundance of the encrusting ascidian *Trididemnum solidum* (Van Name) (BAK *et al.* 1994), reef damage surveys following tropical storm Bret (VAN VEGHEL & HOETJES; 1995), and the monitoring of sea turtle nesting. Other projects, which do not need the guidance of marine biologists, are also carried out by Reef Care. These include the organisation of underwater clean-ups, snorkeling courses for children, Reef Alarm Phone, public lectures and seminars (VAN VEGHEL 1993c) etc..

In this paper the methods (training, experimental design, data collection, data validation) and experiences of working with local volunteers are discussed for Reef

Care's two major research projects, i.e. (1) the coral spawning study and (2) the *Trididemnum* monitoring.

2. REEF CARE'S SCIENTIFIC PROGRAMS

2.1. Coral spawning monitoring

Project type: In coral spawning events volunteer divers monitor the reef during potential spawning periods, both diurnal and nocturnal, and make observations of spawning behaviour of reef organisms. Observations are recorded on special forms or reported to the Reef Care Alarm Phone. Volunteer divers are recruited through the media, viz. local papers and newsletters, radio interviews, flyers and the Reef Care Network. The program was started in 1991 and will now enter its fifth year. The programme expanded throughout the Dutch Caribbean: Bonaire (1992), Saba (1993) and Aruba (1994). Its is our intention to publish the collected data every 5 years.

Training: Each year participants are briefed in a two-hour lecture. The lecture covers: (1) general reproductive biology of corals, (2) results of previous monitoring, (3) species likely to spawn and their spawning behaviour, (4) the kind of data to be collected and (5) how to record spawning data. Slides are shown of species likely to be observed. For details on potential spawning cues see VAN VEGHEL (1994).

Experimental design: In 1991, local divers were asked to swim a 260 m long trail along 284 numbered *M. annularis* colonies at depths between 5 and 15 m (VAN VEGHEL 1993b). The reef on the location 'Slangenbaai' was monitored between about 6:00 p.m. and 1:00 am, 3 consecutive days in August and September (VAN VEGHEL 1993b; 1994). In 1992 and 1993 divers were asked to visit different localities and report sightings on species they observed spawning. In 1994, with a set up similar to 1991, a total of about 125 local divers participated.

Data validation: Volunteers were cross examined about the spawning observations they recorded to confirm that the observations are correct. Slides or film of spawning observations are sometimes made by the volunteers.

Institutional involvement: The project is lead by the senior author, affiliated with the University of Amsterdam (department Tropical Marine Biology), the CARMABI Institute and local dive operators provided logistical support.

2.2. Trididemnum solidum dynamics

Project type: In the *Trididemnum* project diving volunteers monitor the spatial and temporal dynamics of the encrusting compound ascidian *Trididemnum solidum*. This organism contains symbiotic alga, and can overgrow and kill living corals. On

Curaçao reefs the potential threat from this was recognized in 1978 when its distribution and abundance was studied at 42 localities on the leeward reefs (BAK *et al.* 1981; SYBESMA *et al.* 1981; VAN DUYL *et al.* 1981). A comparative study was formulated on Curaçao, (VAN VEGHEL 1993a) and Bonaire (VAN VEGHEL & DE MEYER 1993) for the use of local volunteers, and carried out in 1992. In the second phase of the project permanent quadrats will be established at several representative localities and depths. These will be monitored every 6 months. Every 15 years all 42 localities will be revisited.

Training: Volunteers were trained during a half day workshop, which included a test-dive. A manual was prepared (VAN VEGHEL 1993a; VAN VEGHEL & DE MEYER 1993) and handed out with all the necessary information, and materials (100 m transect line, underwater slates, underwater key to the substrate, 2.5 m line and measurement tape) were provided.

Experimental design: Volunteers were asked to swim two 2.5 m width transects between 1.5 and 35 m deep (tidal range about 20 cm; see VAN VEGHEL 1994) and when a colony of *T. solidum* was observed to record depth, maximum colony length, number of clusters, substrate type (20 categories were listed), and transect length. Volunteers were given the following options for collecting data: (1) at their convenience, and/or (2) at a pre-set time and location during a more social event.

Data validation: The data were checked during control transects by biology students of the University of Amsterdam.

Institutional involvement: Students from the University of Amsterdam (Department of Tropical Marine Biology) carried out control transects and collected data at localities where the species was highly abundant. The Netherlands Institute for Sea Research (NIOZ), the University of Amsterdam and the CARMABI Institute provided logistical support.

3. EXPERIENCES AND DISCUSSION

The success of scientific projects in which data are collected by the volunteers largely depends on the type of the project, the guidance of the scientists involved and the social involvement of the volunteers. The experience with the projects described above gave us a good idea of the potential and limitations of using volunteers and non-professionals in marine science.

3.1. Type of data.

Data collection should be simple: the simplest data are the presence or absence of *e.g.* a reef organism (*Trididemnum solidum*) or a phenomenon (spawning). This requires no special training and can provide essential information. More detailed data collection, *e.g.* number or % of species spawned and size and composition of *T. solidum,* requires extra training and data validation. This is about the level of the present Reef Care projects. Most participating volunteers have no problems working at this level. As an experiment we also asked the volunteers to describe the substrate type on which *T. solidum* was growing, listing 20 potential substrates. However, most volunteers were unable to do this sufficiently accurately despite training during a workshop, the project manual and an underwater identification card. This part of the project was therefore carried out by trained students or collaborating scientists.

3.2. Fieldwork conditions.

When working with groups of volunteers dive safety should come first. Since the work is new and exciting for most participating volunteers (*e.g.* coral spawning) there is a tendency to become more reluctant concerning maximum depth and dive-time. The maximum depth of 35 m in the *Trididemnum solidum*-project should be considered as the absolute maximum depth, although other projects with volunteers go to greater depths (KOBLUK 1991). Since the abundance of *T. solidum* is low between 25 and 35 m, this was not a problem in most transects.

It is our experience that social aspects are an important key to success. During the spawning events of 1991 and 1994 all divers came to one locality, yielding more participants and useful information compared with other years when they were asked to spread to different localities. Also the presence of the scientific coordinator is essential, so that last minute questions can be answered and new people can get a last minute briefing. This was especially useful during the *Trididemnum solidum* monitoring, so that new volunteers could get on-the-job training. In comparison, only 2 out of 42 localities were surveyed on the individual initiative involving 16 divers. During social events 6 to 12 divers attended and up to 3 localities per gathering could be surveyed.

An important difference between the two projects described above is that in the Coral Spawning Project no limitations were necessary in relation to completion of the task and dive-time. However in the *Trididemnum solidum*-project the transect had to be completed according to the methods used in an earlier survey. Problems arose when, at certain localities, the task could not be completed in one dive (sometimes >10 dives were required), because of the increase in abundance of the target species (BAK *et al.* 1994). It is recommended when using volunteers that tasks are chosen so that they can be completed within 1 dive. Continuous monitoring of *T. solidum* dynamics will therefore involve 'small' permanent quadrats of which more than one can be completed in one dive.

3.3. Local versus 'overseas' volunteers.

In contrast to many programmes, Reef Care Curaçao makes use of volunteers that are locally based (WELLS, 1995). In table 1, an overview is given of advantages and disadvantages of local volunteers versus 'overseas'-volunteers (volunteers joining programmes away from their home country). The potential role for each groups is different, and so projects should be adjusted for the type of volunteers involved. The Reef Care programs were carefully selected, i.e. they can be carried out in the evening (Coral Spawning) or weekends as part of a social gathering (*Tridideminum solidum*-project); and they involve long-term monitoring or follow up on unpredictable events (*e.g.* storm damage). These projects make an important contribution to local awareness as a result of press releases, interviews, background articles and television coverage.

Description	**Local**	**Overseas**
In favor of local volunteers		
Logistic costs (transportation, housing, equipment)	low	high
Preparation time of involved scientist(s)	limited	high
Time-span fieldwork	long	short (2 - 4 wks)
Response to unpredicted opportunities	fast	slow
Knowledge of local situation	good	poor
Contribution to local awareness	excellent	limited
In favor of overseas volunteers		
Training	continuously	once
Availability volunteers	mostly week-ends / evenings	continuously
Possibilities for socializing	limited	good

Table 1. Advantages and disadvantages of the use of local versus 'overseas' volunteers in reef assessment studies.

ACKNOWLEDGEMENTS - We would like to thank Dr. Sue Wells and Dr. John W. McManus who provided valuable comments on the manuscript. Paul Hoetjes (Reef Care Curaçao,) and Kalli de Meyer (Bonaire Marine Park) are acknowledged for there logistic support during the projects described above. This contribution was financially supported by Reef Care Curaçao.

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AN ASSESSMENT OF THE USE OF VOLUNTEERS IN CORAL REEF RESEARCH SUPPORTED BY EARTHWATCH

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Abstract - Earthwatch has a long history of supporting coral reef research projects in many geographical areas including Australia, Tonga, Hawaii, the Philippines, the Bahamas, Belize and Israel. A summary of the projects will be presented specifying their objectives, methodology and their success in meeting the objectives. The results of an analysis of how non-scientific volunteers have assisted in the collection of data will be given.

Earthwatch is an international science foundation that sponsors research by finding paying volunteers to help scientists and scholars working on field research projects around the world. This method of support for field sciences, whereby volunteers contribute both their time and funds, is defined as 'participant funding'. Earthwatch is one of the world's largest sources of non-governmental funding for field research. Normally no special qualifications are required to be a volunteer unless diving is undertaken and then volunteers must have the correct certification.

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AN EVALUATION OF THE ROLE OF VOLUNTEER RESEARCH ASSISTANTS ON THE FRONTIER-TANZANIA MARINE RESEARCH PROGRAMME ON MAFIA ISLAND,TANZANIA

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Abstract - This paper describes and critically examines the role that volunteer Research Assistants have played on the Frontier-Tanzania Marine Research Programme on Mafia Island.

The programme was initiated in 1989 against the background of an almost total lack of effective management of coastal zone habitats in Tanzania. In an effort to rectify the situation, steps were initiated to establish Tanzania's first marine national park at Mafia Island. The dependence of several human communities on utilisation of marine resources in Mafia's waters warranted development of a management plan based on the concept of integrated multi-user management. The accompanying demand for significant quantities of detailed information on the physical and biological environment and on resource utilisation was met, in the absence of available expertise in Tanzania, with a programme of intensive data collection by supervised ex-patriate volunteer research assistants.

With this aim, the Frontier-Tanzania Marine Research Programme has completed more than four years of detailed survey work around Mafia Island enabling the formulation of a suitable management plan. Implementation of the marine park has since attracted the support of other international bodies and it is expected that the park will be gazetted by the end of 1994. Data gathered by volunteers is also provided to a UNEP regional East African marine database initiative and to the World Conservation Monitoring Centre.

Since the programme began, in excess of 5000 diving man-hours have been devoted to sub-tidal work. SCUBA activities thereby comprise a main component of volunteer research schedules. Baseline surveys have been conducted for all major habitats, including coral reefs, seagrass beds, inter-tidal zones and mangrove stands. Using appropriate transect and quadrat sampling techniques, attention has focused on species diversity, species abundance, condition, and structure and form of each habitat. Considerable man-hours have further been devoted to longitudinal reef-fish surveys involving identification and counting of selected indicator fish species; and surveys recording location, type and extent of damage to hard corals. Equivalent priority has been accorded to a parallel programme of resource-use surveys, requiring volunteers to gather data in direct interaction with local fishermen and women. Surveys have concentrated on calculating catch-per-unit effort ratio and catch composition for all types of fishing gear utilised by local fishing communities, including shark netting, seine netting, long line fishing, fence and box traps, and opportunistic hunting and collection of octopus, crabs and gastropods. Additional surveys of the extraction and utilisation of coral for building, and of subsequent regeneration of corals have also been undertaken.

Secondary studies have been carried out to assess observer error amongst unskilled volunteers. Sub-tidal observer error trials were aimed at determining the precision and reliability of fish identifications and fish counts by volunteers using visual census techniques, and also of underwater estimation of length and frequency distributions. Volunteers were further evaluated for their suitability in applying the principles of baseline surveys to a longitudinal monitoring programme. A study was also carried out to assess consistency of accuracy amongst volunteers undertaking repetitive vegetation plot measurements in mangrove stands. Comparisons of observer error amongst unskilled volunteers with that of professional marine biologists demonstrate that use of volunteers can generate credible research data and be an effective resource for conservation research activities. The extent to which this is true depends in part on techniques applied to selection, preparation and supervision of volunteers. Recommendations are made for further work in developing optimum techniques for such volunteer management.

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CULTIVATING CITIZEN STEWARDS FOR THE MARINE ENVIRONMENT: THE NATURE CONSERVANCY'S EXPERIENCE IN FLORIDA

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Abstract - The Nature Conservancy is a U.S.-based non-profit membership organization whose mission is to preserve plants, animals, and natural communities that represent the diversity of life on Earth by protecting the lands and waters they need to survive. Traditionally, the Conservancy's work focused on the protection and management of natural lands; however, in places like South Florida and the Caribbean, the Conservancy is now turning to address threats to diverse marine environments.

Forty years of experience in the United States has taught the Conservancy that many citizens are motivated to contribute their services as volunteer "stewards" of sensitive lands. Furthermore, these people, though from diverse backgrounds, are capable of learning and performing technically demanding tasks. As an example, The Nature Conservancy's Volunteer Stewardship Network in northeastern Illinois includes more than 5,000 volunteers who perform tasks ranging from monitoring rare insect populations to conducting prescribed fires on remnant prairies.

Over the course of the past three years, The Nature Conservancy has collaborated with other institutions to create volunteer science and stewardship programs for marine protected areas, particularly in the Florida Keys. Coral Watch, Florida Bay Watch, and Reef Fish Surveys are among the programs now providing valuable data to protected area managers. These programs open opportunities

to engage in ecological survey and monitoring programs that would be prohibitively costly if limited to paid personnel. To be successful, however, such programs require substantial investments in designing appropriate protocols, coordinating and training volunteers, and ensuring the quality of the data collected.

Cooperation with other institutions that share Conservancy goals but provide complementary capabilities has been crucial. Examples include:

- Establishing the Florida and Caribbean Marine Conservation Science Center with the University of Miami. Center staff design monitoring protocols, provide training and technical support, test and assure the quality of data, and manage and interpret data Conservancy staff in field offices (like Florida Keys office) can then concentrate on recruiting and supervising volunteers.

- Assisting the Reef Environmental Education Foundation (REEF) in developing protocols for conducting fish surveys with volunteers. REEF personnel recruit, train, and supervise volunteer divers. Data are managed and interpreted at the Florida and Caribbean Marine Conservation Science Center.

- The Florida Keys National Marine Sanctuary is a partner in a volunteer program that provided over 5,300 hours in 1993 in a wide range of tasks supportive of the Sanctuary's goals to protect marine life in the Keys. The program coordinator is a Nature Conservancy employee, but works in the Sanctuary office.

- Florida Bay Watch engages volunteers in seven data collection protocols designed in cooperation with scientists from several academic institutions and public agencies. The professional scientists participate in data collection alongside the volunteers in some cases, in others they receive and process samples, sharing their results through Bay Watch Publications. Funding comes from a network of public and private institutions.

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EFFECTIVENESS OF TRAINED VOLUNTEER RECREATIONAL DIVERS IN RESEARCH STUDIES OF ARTIFICIAL REEFS

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Abstract - As part of a broader program in research and technology transfer dealing with artificial habitats in the coastal ocean, in an evaluation of field techniques we hypothesized that with proper training in scientific procedures, scuba divers who are members of recreational dive organizations can make reliable, accurate measurements of certain parameters. In 1990-1991 over 40 members of the Reef Research Team repeatedly made 10 physical and biological measurements of five artificial reefs in the Atlantic Ocean 20-35 m deep and within 30 km off the coast of Jacksonville, Florida, USA. Results from 222 dives indicate high consistency and accuracy of determinations of temperature, thermocline, depth, salinity, visibility, sediment texture and reef boundaries among divers specifically assigned to such tasks, and less consistency for determining sediment depth and censusing of fishes. Greater and unacceptable variability in data occurs when dive teams are assigned too many concurrent tasks.

Labor intensive field data collection at artificial reef sites can be enhanced when trained volunteer divers participate. Performance is improved when the number of tasks are limited and assigned for each pair of divers or a particular diver. It is important to have scientific personnel participate in planning field projects involving volunteers and in analysis of data. (Documents concerning logistics of the volunteer organization and training techniques are provided for review by workshop attendees).

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THE DEVELOPMENT AND STATUS OF THE CORAL CAY CONSERVATION SCIENTIFIC PROGRAMME

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Abstract - Since its inception in 1986, Coral Cay Conservation (CCC) has used over 1000 volunteer divers in a programme to assist the Coastal Zone Management Unit (CZMU) of Belize, Central America. Following an intensive 8-day period of training, volunteers carry out baseline surveys using a rapid technique which seeks to describe benthic topography, habitat types and species assemblages using ordinal abundance estimates on a scale of 0-5. The technique has been steadily refined as better technology has become available (eg. differential global positioning systems) and as the capability of volunteers has been increasingly understood. For example, the scope of surveys for Scleractinia, fish and macroalgae has advanced from a family/genus level of identification to a species level.

CCC considers evaluation of the accuracy and precision of survey data to be of primary importance. A validation study has demonstrated that the precision of ordinal abundance estimates is within the range stipulated for statistical analysis. A visual fish census technique is currently being refined following the results of a validation exercise. The feasibility of using standard quadrat methods for assessing reef communities at a species level is also being examined.

Baseline data collected by CCC volunteers are used to interpret aerial and satellite imagery and through the application of vector geographic information systems, CCC has provided essential information on the nature and extent of marine resources throughout several areas of the Belize Barrier Reef. The resulting resource maps have been used in the preparation of management plans for both the proposed Sapodilla Cays Marine Reserve and the proposed South Water Cay Marine Reserve. Data currently being gathered will be used in the preparation of management strategies for other areas of the coastal zone.

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THE USE OF VOLUNTEERS IN CORAL REEF SURVEYS: THE "REEFWATCH" EXPERIENCE

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Abstract - The Reefwatch scheme developed from about 1980 in response to requests from University student expeditions and amateur SCUBA divers for advice on what studies they could undertake during visits to coral reef areas. The complexity of reef ecology and the difficulty for amateurs of identifying the diverse reef fauna necessarily limited the scope of what might be attempted. Consequently a standard set of recommendations were developed involving:

a) completion of a basic reef description form, and b) counts along belt transects of some more easily recognized indicator groups (butterflyfishes, groupers and sea urchins). In some instances valuable data has been collected leading to identification of priority areas for conservation (*e.g.* in the Turks and Caicos) or evidence of broad-scale ecological relationships (*e.g.* between echinoids and fish predators). More recently some of the methods in improved form have been found valuable in enabling rangers in Marine National Parks (*e.g.* in Egypt and Kenya) to monitor reef populations. On the other hand there have commonly been problems in finding resources for analysis and reporting, and in some cases the quality of data collected has been inadequate. Volunteers may fail to spot some of the species being counted or even score false positives as a result of misidentification. Problems have also been encountered with semi-subjective estimates of reef quality although more reliable protocols for making semi-subjective assessments of coral assemblage character and estimates of coral abundance have now been developed. Experience indicates that volunteers can generate valuable data provided basic training is given on site by an experienced worker and that the accuracy of counts and estimates is audited. A number of training procedures have been developed enabling observers to familiarise themselves with both target species and others with which they might be confused (*e.g.* species encounter versus time plots), and to improve the accuracy of their counts (*e.g.* independent return counts along transects immediately following supervised outward counts). There is however an urgent need to establish an internationally recognized system of training and qualification which will enable more convenient and reliable use to be made of the consider able resource that volunteer observers represent.

SCLERACTINIANS

SOME NEW SUGGESTIONS ON FUNCTIONAL MORPHOLOGY IN PENNULAR CORALS

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Abstract - A pennular septum usually displays regular, successive, bilateral pairs of expansions having a common level on both sides of the septum. In places, these expansions appear vertically shifted in two halves (two mi-pennulae). This removal apart has been attributed to stresses and strains on the secretory epithelium. Two concrete reasons are suggested here: 1) The readjustment of alternation between neighbouring pennular rims following an introduction of a new septum 2) The readjustment of pennular positions in the case of curving of septa.

1. INTRODUCTION

Pennular corals are very common in Mesozoic sediments, yet their genuine architecture is recognized earlier, in Palaeozoic (Devonian) rugose corals and later, in younger Tertiary and Recent forms (GILL & RUSSO 1980). Recently, SCHLICHTER & FRICKE (1990;1991) and SCHLICHTER (1991;1992) have discovered an unexpected physiological adaptation within the living pennular, zooxanthellate coral *Leptoseris* - that of a relatively deep-water suspension feeder. As pennular architecture is highly characteristic can the particular life habit disclosed in *Leptoseris* be extrapolated to all fossil pennular taxa ? For the moment it remains an open question, yet, it seems likely to admit for them a suspension feeding habit, as the ledges formed by the pennulae serve to hold in position the particular gastrovascular tubes observed within the suspension feeder *Leptoseris*. In revenge, the habit of dwelling in depth under poor luminosity (by the aid of light amplifying pigments in the case of *Leptoseris*) is not supported in fossil pennular corals by direct, material, functional evidence. However, depth indication is not to exclude since fossil pennular corals are frequently found exclusive in communities embedded in totally or partially fine grained, calm water sediment. The pennular pattern might thus turn, after a sound global environmental analysis, to a helpful morphofunctional tool for palaeoecological interpretation. Communities dominated by pennular species may undoubtedly be interpreted as the deepest zooxanthellate coral assemblages (GILL & LATHUILIERE in preparation). SCHLICHTER & FRICKE (1990;1991) and SCHLICHTER (1991; 1992) have recorded the occurence of living *Leptoseris fragilis* between 95 and 145 m depths. *Leptoseris hawaiiensis* has been reported to be living in deeper water down to a record depth of 470 m (VAUGHAN 1907). This last value seems however excessive as equivalent values have not been communicated since.

Hence, there are grounds for supposing that the palaeoecology of pennular corals may become a clue to palaeobathymetric reconstruction of Mesozoic coral-bearing beds and reefs. In this short note we suggest a new key to understand the morphological mi-pennular character through a functional approach.

2. POSSIBLE CAUSES TO THE OCCURRENCE OF MI-PENNULAE

Longitudinal sections perpendicular to pennular septa show two types of pennular development. The first, the more common, displays pennulae with both sides in continuity on the same level (Fig.1 left, Pl.1 Fig.1).

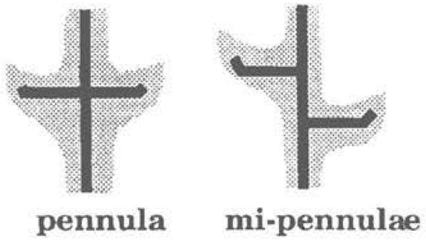

Fig.1. Pennula and mi-pennulae in longitudinal section perpendicular to septal plane.

The second type shows partition in two halves, displaced vertically from each other. In this case we speak of mi-pennula to designate each single half (Fig.1 right, Pl.1 Fig.2). The degree of displacement between the two halves may vary from very slight to strongly pronounced. In both types, the alternation between pennular lateral rims of neighbouring septa is observed (Pl.1 Fig.5). The regular pennula seems to represent the normal state of development (GILL 1982), whereas the mi-pennular state would be a response to occasional stress (GILL 1967, Fig.6b).

We have imagined several circumstances which would induce mi-pennular development. The most probable cause would be the insertion of a new septum. A most stable feature within pennular corals is the alternation of pennular levels between adjacent septa. The introduction of a new septum between two pre-existing ones will require henceforward a general readjustment. The two pre-existing septa which were in alternation to each other will have to share, after re-equilibration, the same level while being in alternation with the newly inserted septum between them. The re-equilibration is facilitated by controlled shifting of the mi-pennulae which may develop all across the zone of insertion (Fig. 2).

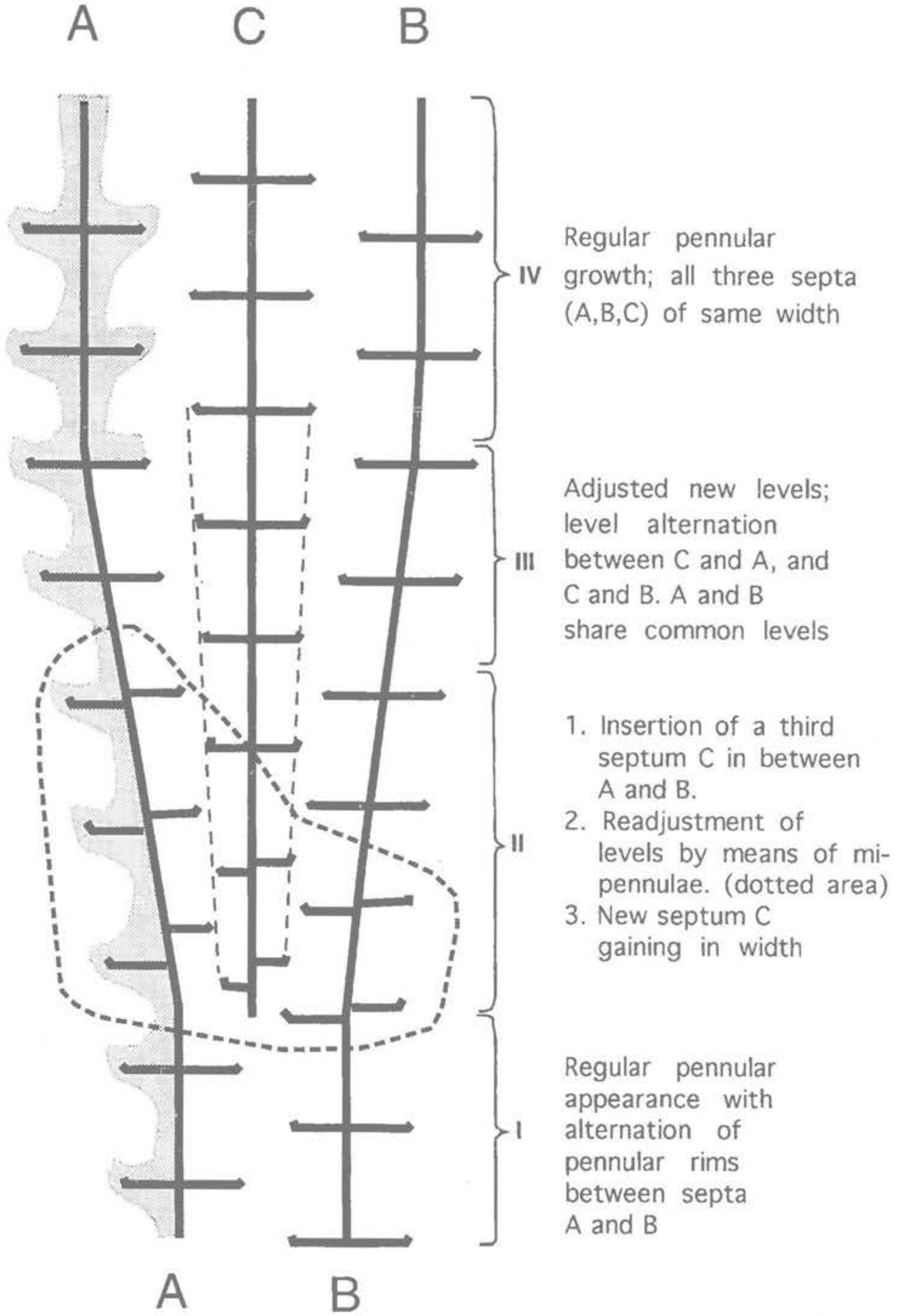

Fig.2. Insertion of new septum C and the readjustment involved through differential mi-pennular development

Another cause may be the curving of septa which will differentiate pennular distances. Here too, passing to mi-pennular pattern will readjust the system.

Pl.1 Figs.3, 4, 6 show sections which can be interpreted in such a manner.

According to this logic mi-pennulae will be rather absent in zones without insertion of new septa or septal bending.

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Plate 1

Longitudinal, perpendicular to septal planes thin sections.

Fig. 1.Three well-balanced symmetrical pennulae alternating in level with pennulae of the adjacent septa. *Periseris*, Bajocian of Malancourt France, (MC1) x 80.

Fig. 2. Mi-pennulae (seven) swaying along a trabecular axis. Same specimen as in fig.1 x 80.

Fig. 3. Formation of mi-pennulae incited probably by insertion of a new septum. *Dimorpharaea*, Oxfordian of Foug, France, (FOU 29) x 19.

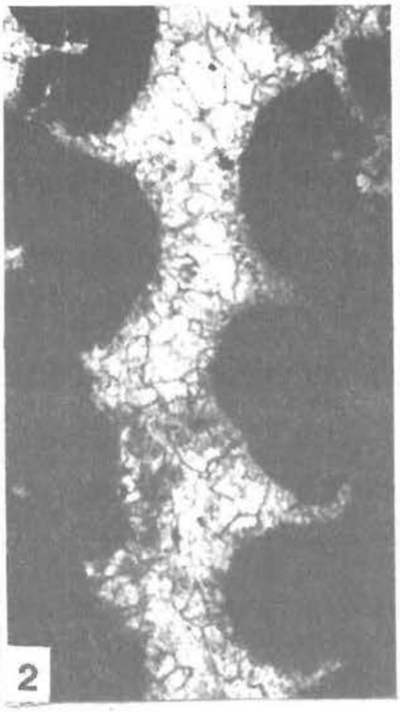
Fig. 4. The presence of mi-pennulae seems attributable here to septal bending. The bending accompanies a distal numerical diminution of septa. *Periseris*, Bajocian of Marbache, France, (MAR 18) x 13,5.

Fig. 5. Alternation between pennular rims of adjacent septa applies whatsoever to pennulae or mi-pennulae. *Periseris,* Bajocian of Viterne, France, (VF 10). ~x.15.

Fig. 6. Mi-pennulae probably related to insertion of a new septum. *Periseris,* Bajocian of Créancey, France, (CRE 28) x29.

Plate 1


1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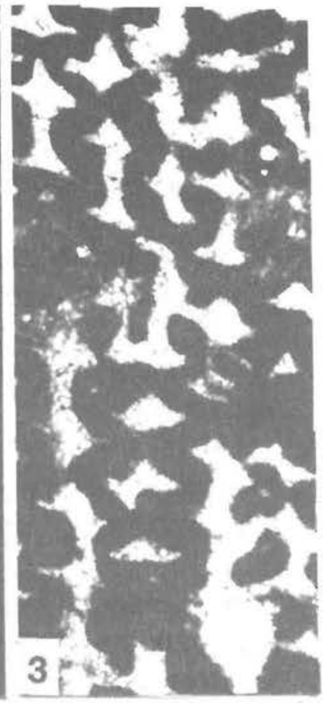
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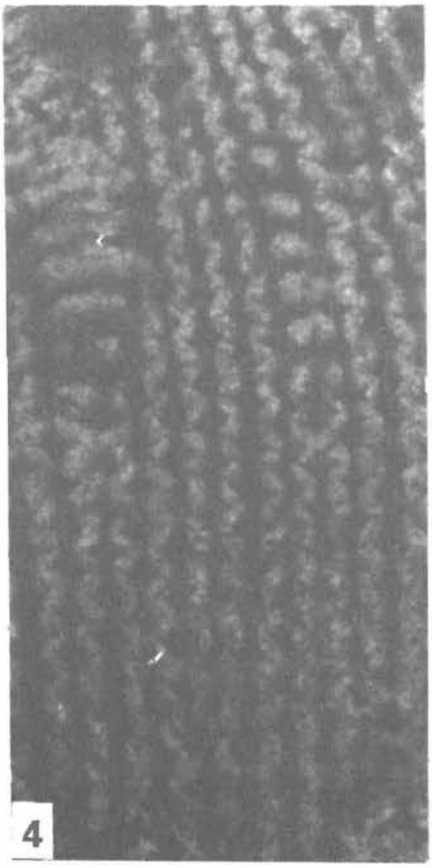
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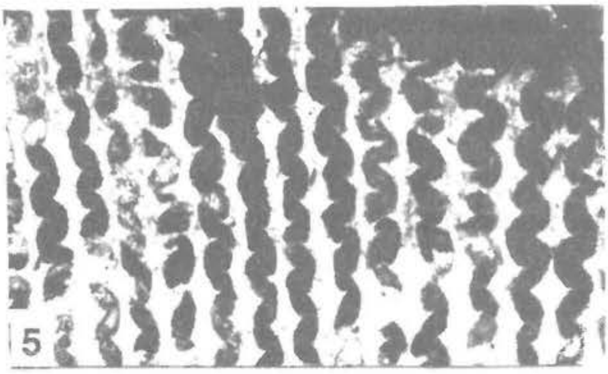
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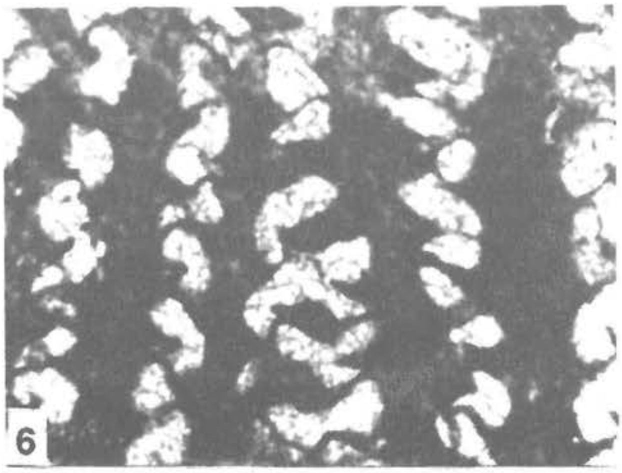
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A HIERARCHICALLY STRUCTURED LIST OF SCLERACTINIAN CHARACTERISTICS - A PROPOSAL

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Abstract - During a workshop on Scleractinia in Paris 1993, BEAUVAIS *et al.* proposed a " Catalogue standard de morphologie des Madréporaires". It soon became clear that this list had to be structured hierarchically for practical use: items lined up in a parallel manner frequently represent subcategories of each other or are mutually exclusive. However, the"catalogue" has been translated into English and German in the meantime but no attempt has been made so far to clarify its logical structure.

The proposed list handed out to the participants of the workshop "Scleractinia" is presented and explained in the talk. The aim of the revision of the original "catalogue" is to guide authors through the morphological terms to be used in the description of Scleractinian corals.

Using the terms of the English version of the "catalogue" (ROSEN 1993; Fossil Cnidaria 22 /2), its items are here grouped in logically coherent units. Their hierarchy is expressed by simple symbols. Despite the improvements, the proposed list is understood as very preliminary: none of the necessary additions to the "catalogue" have been made here because the extent of these additions is still under discussion. Only presence/absence items have been incorporated as well as some sections have been amalgamated. For better comparability, the revision stays closely to the original; the final version would certainly have to be better readable.

A HIERARCHICALLY STRUCTURED LIST OF SCLERACTINIAN CHARACTERISTICS

Morphology of the Corallum (A,B)

- attachment of skeleton (A4)
- kind of corallum (A1) :-shape of solitary corallite (A2)
  - -rejuvenescence (B5)
  - -calicular platform (C3) : infundibuliform calicular platform (C4)
  - :-shape of colony (A3)
  - -arrangement of calices(A6) : small pillars (A7)
    - : large central calice (A8)
    - :-orientation of series (A9)
    - -form of series (A10)
    - -length of series (A11)
    - -opening of series (A17)
    - -isolated calices (A12)
    - -form of collines (A13)
    - -continuity of collines (A14)
    - -height of collines (A16)
    - -ambulacra (A15)
    - -distinctness of calices (A1 8)
  - -budding (B1) : extracalicular budding (E2)
    - : intracalicular budding (B3) polystomodaeal budding (B4)
  - -calicular platform (C5)

Calice (C)

- distinctness of calicular margin (C1)
- width of calicular margin (C2)
- distribution of calices (C6)
- form of calices (C7)
- calicular diameter (C8)
- calicular distance (C9)

External Surface (D,E)

- presence of epitheca
  - :-thickness of epitheca (D1)
  - ornamentation of epitheca (D2)
  - presence of costae (D3)
    - :-arrangement of costae (D4)
    - density of costae (D5)
    - relation to radial elements (D6)
    - distal ornamentation (D7)
    - lateral ornamentation (D8)
    - basal expansion of costae (D9)
    - : replacement of costae (D10)
- presence of peritheca
  - formation of peritheca (E1)
    - : costate peritheca (E2)
  - width of peritheca (E3)
  - surface of peritheca (E4)

- presence of coenosteum (E5,E6)

Radial Elements (F,K)

- kind of radial elements (F1)
  - :angle of divergence (F2)
- confluence (F3)
- compactness of radial el. (F4)
  - : -position of perforations (F5)
  - density of perforations (F6)
- general symmetry (F7)
  - : type of radial symmetry (F8)
  - : type of bilateral symmetry (F9)

- systems (F10)
  - : number of cycles (F1 1)
  - : number of radial elements (F12)
- density of radial elements (F13)
- projecting septa (F14)
- lonsdaleioid septa (F15)
- relationship of radial elements (F16)
- transverse section of radial elements (F17)
- thickness of radial elements (F18)
- straightness of radial elements (F19)
- maximum relative length of radial elements (F20)

- lateral faces of radial el.(F21)
  - : -regularity of ornamentation (F22)
  - size of ornamentation (F23)
  - density of ornamentation (F24)
  - arrangement of ornamentation (F25)
- distal margin of rad. el.(F26)
  - :-size of dentations (F2 7)
  - regularity of dentations (F28)
  - shape of dentations (F29)
- different ornamentation of different cycles (F30)
- external margin of septa (F3 1)
  - : size of dentations (F32)
- internal margin of septa (F33)
  - : septal spines (F34)
  - : paliform teeth (F35)
  - : pali (F36)
- microstructure of rad. el. (K1)
  - :-structure of trabeculae (K2)
  - size of trabeculae (K3)
  - vertical relationship of trabeculae (K4)
  - radial direction of trabeculae (K5)

-vertical continuity of trabeculae (IC6) : dissociation (K7)
-growth lamellae (K8)

Axial Structure (G)
-presence of columella :- origin of columella (Gl) :essential columella (G2): lamellar essential columella (G3)
: parietal columella (G4)
-arrangement of columella (G5)
-calicular pit (G6)

Endotheca (H,K)
-presence of dissepiments :- distribution of dissepiments (H 1) : zonal dissepiments (H2)
-density of dissepiments (H13)
-microstructure of dissepiments / primary layer (K9)
-microstructure of dissepiments / lower layer (K10)
-microstructure of dissepiments / upper layer (Kl 1)
:-shape of dissepiments (H3)
-number of dissepiments (H4)
-thickness of dissepiments (H5)
:-shape of dissepiments (H6)
-number of dissepiments (H7)
-thickness of dissepiments (H8)

-presence of tabulae :-distribution of tabulae (H9)
-shape of tabulae (Hl 1)
-number of tabulae (H10)
-thickness of tabulae (H12)
-microstructure of tabulae (K12)

Synapticulae (I)
-presence of synapticulae :-type of synapticulae (Il)
-density of synapticulae (12)
-distribution of synapticulae (13)

Wall (J)
-presence of wall :-wall type (Jl)
-wall structure (J2) : parathecal wall (J3)
: septothecal wall (J4)
: synapticulothecal wall (J5)
: trabecular wall (J6) : elementary-trabecular wall (J7)
-wall thickness (J8)
-wall porosity (J9)
-mural extensions (JlO)

explanation of symbols: - following item is relevant for all conditions of the (sub)category
: following item is relevant only for parts of higher category

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QUANTITATIVE MORPHOLOGY OF NEOGENE FREE-LIVING CORALS (SCLERACTINIA) FROM FLORIDA AND THE DOMINICAN REPUBLIC

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Abstract - Free-living scleractinian corals form a major constituent of Mio-Pliocene Caribbean coral communities in both reef and reef-marginal environments. Previous research using a compilation of reef coral occurrences in the Caribbean has documented a high rate of turnover during the Late Pliocene to early Pleistocene, with free-living taxa especially affected. To assess whether these patterns are not merely taxonomic artifacts, we have developed an improved morphometric technique for distinguishing among species-groups in pseudo-solitary members of the Trachyphylliidae.

Material was studied from both the well-documented Late Miocene deposits of the Northwest Dominican Republic and the Late Pliocene Pinecrest sandstone from Southern Florida (USA). Point coordinates from a set of 23 landmarks were obtained from orthogonal photographs of the oral surface of each colony. The landmarks were constructed relative to the distinctive double bilateral symmetry of these colonies, so that each colony was described by four symmetrical constellations of nine points. These coordinates were subsequently translated, rotated in the plane, and scaled to form a set of 14 shape coordinates. A subset of mean shape coordinates for colony halves was used to distinguish three large groups of morphologically distinct colonies using average-linkage cluster analysis. The groups were then refined using iterative discriminant analysis with discrimination models evaluated using joint membership of colony halves. Examination of plots of mean shape coordinates for each group indicated that the groups differ mainly by the roundness and degree of constriction of the calical margin, as well as columellar length and width. Group A includes elongate colonies with poorly defined lateral lobes and relatively long, narrow columellae, while group B is composed of colonies with well-defined lateral lobes and elongate columellae. Colonies with circular calical margins and relatively wide columellae are mainly assigned to group C. All three groups were found in the material from the Dominican Republic, but group C is absent from the studied Pinecrest material. Analysis of colony heights measured along growth axes indicates that group C includes smaller colonies than groups A or B, suggesting that group C includes juvenile forms.

The results of this study suggest that at least two species of pseudo-solitary corals from the Trachyphylliidae occur in the study units. Examination of type material and previously published species description suggests that group B corresponds to *Trachyphyllia bilobata* (Duncan 1863) and group A represents *Antillophyllia sawkinsi* (Vaughan *in* Vaughan & Hoffmeister 1926). At present, the taxonomic status of the third group remains unclear. The recognition of *A. sawkinsi* from the Pinecrest Sandstone would extend its range into the Late Pliocene suggesting that the magnitude of Pliocene-Pleistocene Caribbean coral extinction is greater than has been previously estimated.

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SCLERACTINIAN SEPTAL MICROSTRUCTURES : TAXONOMICAL ASPECT

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Abstract - The microstructure of septa is a diagnostic feature which permits to classify genera and families into higher-rank taxa. It is possible to differentiate two main micro-structural types: **I**. fascicular, i.e. non-trabecular (suborder Stylophyllina) and **II**. trabecular (remaining corals) with (A) simple, (B) compound and (C) divergent trabeculae. Depending on the diameter of trabeculae one can distinguish: minitrabeculae (d up to ca 50 µm), medium-sized trabeculae (from ca 50 to ca 100 µm) and thick trabeculae (usually more than 100 µm). The character of septal ornamentation depends upon the microstructure: in the type I distal margins are coarsely ornamented and sides smooth; in the type II distal margins are either smooth, or denticulated or moniliform and sides covered with granulations, pennules a/o menianes.

Differentiation of trabecular structures in the type II is as follows:

(A). Simple-trabecular pattern is based on monoaxial main trabecula with the following variations:

1. nonbranching minitrabeculae (Caryophylliina; Faviidae: minitrabecular septal portions);

2. main trabecula with lateral fascicles of fibres coalesced into menianes, diameters shifted to medium size (Astraeomorphidae, Procyclolitidae);

3. medium-sized main trabecula with facultatively developed fascicles pronounced as irregular granulations (Pachythecaliina).

(B). Compound, i.e. branching trabeculae show three main patterns:

I. monoaxial main trabecula (= primary trabecula) sending: (a) secondary trabeculae represented by granulations (*e.g. Chondrocoenia, Isastrea, Ironella, Mesomorpha, Haplaraea*), or by pennulae or menianes when coalesced with each other (*e.g. Thamnasteria*); (b) non-axiferous fascicles of fibres producing menianes (*e.g. Stuoresia, Tropidendron*);

2. polyaxial primary trabecula giving secondary trabeculae (*e.g. Favia, Mussa, Dimorphocoenia*);

3. main trabecula composed of fascicles of fibres and/or axes sending around well delimited fascicles which coalesce to form pennules and menianes (Latomeandridae, Microsolenidae, Cunnolitidae, Synastreidae). Diameters medium-sized and thick.

(C). Divergent trabeculae are composed of segments arranged in a zigzag pattern, each of the segments terminating with a granulation (*e.g.* in *Porites* and *Columnocoenia*). Diameters medium-sized. Some special structures, such as pali (Faviidae, Caryophylliina), auriculae (Stylinina, Rhipidogyrina), or regular septal porosity (*e.g.* Microsolenidae, Haplaraeidae) are limited to corals of particular trabecular types.

Microstructural differentiation of early scleractinians (Anisian-Ladinian: types I, II A1-3, B1) justified the opinion concerning their polyphyletic origin.

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MORPHOLOGICAL AND MICROSTRUCTURAL OBSERVATIONS ON THE ONTOGENY OF CARYOPHYLLIIDS; TERMINOLOGICAL ASPECT

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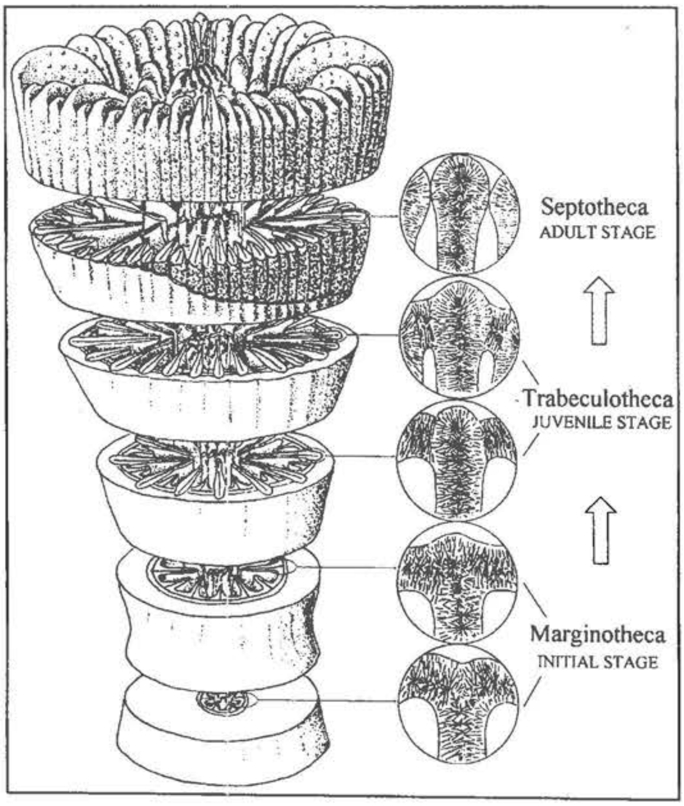
Abstract - In the Caryophylliina radial elements are built by a medially situated row of minitrabeculae (d from ca. 15 to 50 µm). In their classification an important role play types of thecal structures. There are very few observations and interpretations of the ontogeny of thecal microstructures.

In the ontogeny of caryophyllids three main stages can be distinguished : **(1)** The initial stage starts with the basal plate, and ends with a distinct constriction of the corallum diameter. All investigated forms (e. g. *Caryophyllia, Desmophyllum, Paracyathus, Parasmilia*) have in this stage a marginothecal wall (MORI & MINOURA 1980). Minitrabeculae of the wall are coalescent with a trabecular palisade of the septa. The septa and wall are formed simultaneously and there is no evidence of presence of the solitary 'euthecal' ring. Usually, in the later growth the original very thin skeleton is covered by thick exothecal sclerenchymal tissue and often also filled by endothecal sclerenchyme (=stereome). **(2)** The juvenile stage starts with an enlargement of the corallum diameter. The development of radial structures (costae) causes interruption of the marginotheca and the formation of a trabeculothecal wall (sensu CHEVALIER 1987). The trabeculotheca consists of interseptal segments of minitrabecular nature. Thickening of the septa and reaching their ultimate number (for particular species) usually is combined with vanishing of trabeculothecal segments and formation of the septotheca in the **(3)** adult stage. In neotenic groups of caryophyllids (i.e. flabellids) the marginothecal wall is present in the whole ontogenetic sequence.



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