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Distribution and Environmental Control of Coral Assemblages in Northern Safaga Bay (Red Sea, Egypt)

Bernhard **Riegl** and Werner E. **Piller**, Wien

KEYWORDS: CORAL ASSEMBLAGES – ASSEMBLAGE MAPPING – ENVIRONMENTAL CONTROL – ECOLOGY – CORAL REEF – CORAL CARPET – SAFAGA, RED SEA (EGYPT) – HOLOCENE

CONTENTS

SUMMARY

Coral assemblages in northern Safaga Bay, Red Sea, Egypt, are qualitatively described. Nine distinct assemblages were found, which correspond to quantitatively defined community types previously described from the area off Hurghada, northern Red Sea. Their distribution within northern Safaga Bay was mapped. Strong gradient and/or steep relief assemblages were: *Acropora* assemblage on windward (exposed) reefs, *Porites* assemblage on leeward (sheltered) reefs, *Millepora* assemblage on current exposed reefs, *Stylophora* assemblage on reef flats. Low gradient and/or low relief assemblages were: *Acropora* dominated coral patches in areas of good circulation to a depth of 15 m, *Stylophora*/*Acropora* coral patch assemblages in shallow sheltered environments, faviid carpet in low relief areas between 10 and 25 m which with increasing turbidity turns into a depauperate faviid carpet, *Porites* carpet in low relief areas between 5 and 15 m with clearest water, *Sarcophyton* carpet in low relief areas with high suspension load, platy scleractinian assemblage in deeper water (>25 m) with low light intensity. The distribution of coral assemblages depends basically on 1) topography 2) hydrodynamics 3) light and 4) suspension load.

1 INTRODUCTION

Due to their overwhelming ecological importance in tropical marine ecosystems and their relatively good fossilisation potential, frequent attempts have been made to use corals (and coral-like organisms like Tabulata) as indicators for paleo-environments (e.g., Frost, 1981; Pandolfi, 1984; Fagerstrom, 1987; Pandolfi & Burke, 1989; Geister, 1992; Bosellini & Russo, 1994; Bosellini & Perrin, 1994). The criteria applied are frequently deduced from findings obtained in comparable modern systems (Rosen, 1977). It is therefore important to study organisms in their modern environment from a geologic/paleontologic perspective: a process known as actuopaleontology (Dodd & Stanton, 1990).

In an integrated study in northern Safaga Bay, Red Sea, Egypt (Fig. 1), different facies and sedimentary environments were investigated (Piller & Pervesler, 1989; Piller & Mansour, 1990; Kleemann, 1992; Nebelsick, 1992; Piller, 1994). The aim was to produce data strongly oriented towards a paleo-ecological aspect which would allow Recent as well as fossil communities to be interpreted.

We wanted to know 1) Whether distinct coral assemblages could be found. These assemblages should be definable in such a way, that they could be recognized in the Cenozoic where taxonomic uniformitarianism is applicable, as well as in older earth history, where this approach cannot be used but structural typology can be used for definition

Addresses: Dr. B. Riegl, Prof. Dr. W. Piller, Institut für Paläontologie, Universität Wien, Geozentrum, Althanstr. 14, A-1090 Wien. Fax: ++43-1-31336-784, e-mail: wep@pal.univie.ac.at. Present address B. Riegl: Gulf of Aqaba Protectorates Development Project, Egyptian Environmental Affairs Agency, Department of Natural Protectorates, 23A Ismael Mohamed Street, Zamalek, Cairo, Egypt

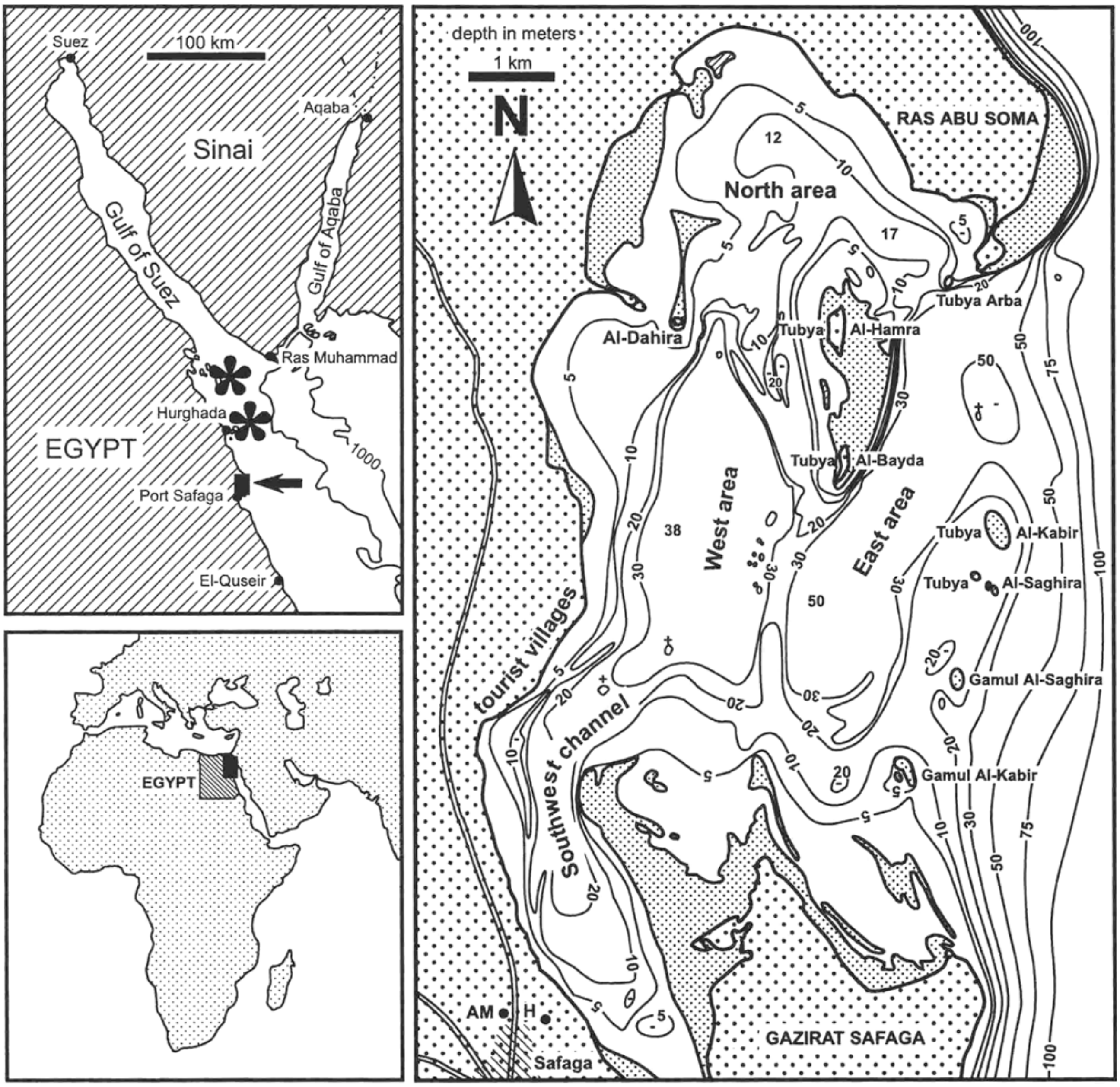


Fig. 1. Location map of northern Safaga Bay, Red Sea. The asterisks in upper left figure indicate the area of quantitative sampling in RIEGL (1989) and RIEGL & VELIMIROV (1994).Right figure: Land – coarse stippled, tidal flats – fine stippled.

instead. 2) Whether a distinct spatial pattern of coral assemblages is observable. 3) Whether assemblages are comparable to those observed from other areas in the Indo-Pacific (ROSEN, 1971, 1975; DONE, 1982; PERRIN et al., 1995). 4) Which are the main factors influencing and shaping these assemblages.

2 METHODS

The assessment of coral assemblages in Safaga Bay was primarily based on quantitative results obtained in earlier work by KLEEMANN (1992) in Safaga Bay and by RIEGL (1989) and RIEGL & VELIMIROV (1994) between Gubal saghir Island (Gubal Straits, southern Gulf of Suez) and Sal Hashish Island (Abu Hashish) approximately 50 km north of Safaga Bay (Fig. 1). The proximity of the latter areas to the presently investigated reefs (Fig. 1), and a similar oceanographic setting, suggested that equivalent coral assemblages should occur. The above mentioned authors used the 10 m line transect method (LOYA, 1978) to quantitatively describe patterns in coral communities. The observed community zonation was very clear (Table 1) and during the present study it was possible to recognize these communities without quantitative sampling. Coral assemblages were characterized and could be recognized by their dominant species, overall species composition, space coverage, and diversity. Therefore it was possible to visually survey coral assemblages in Safaga Bay. As their differentiation was very clear, it was not necessary to repeat quantitative sampling, which would have limited

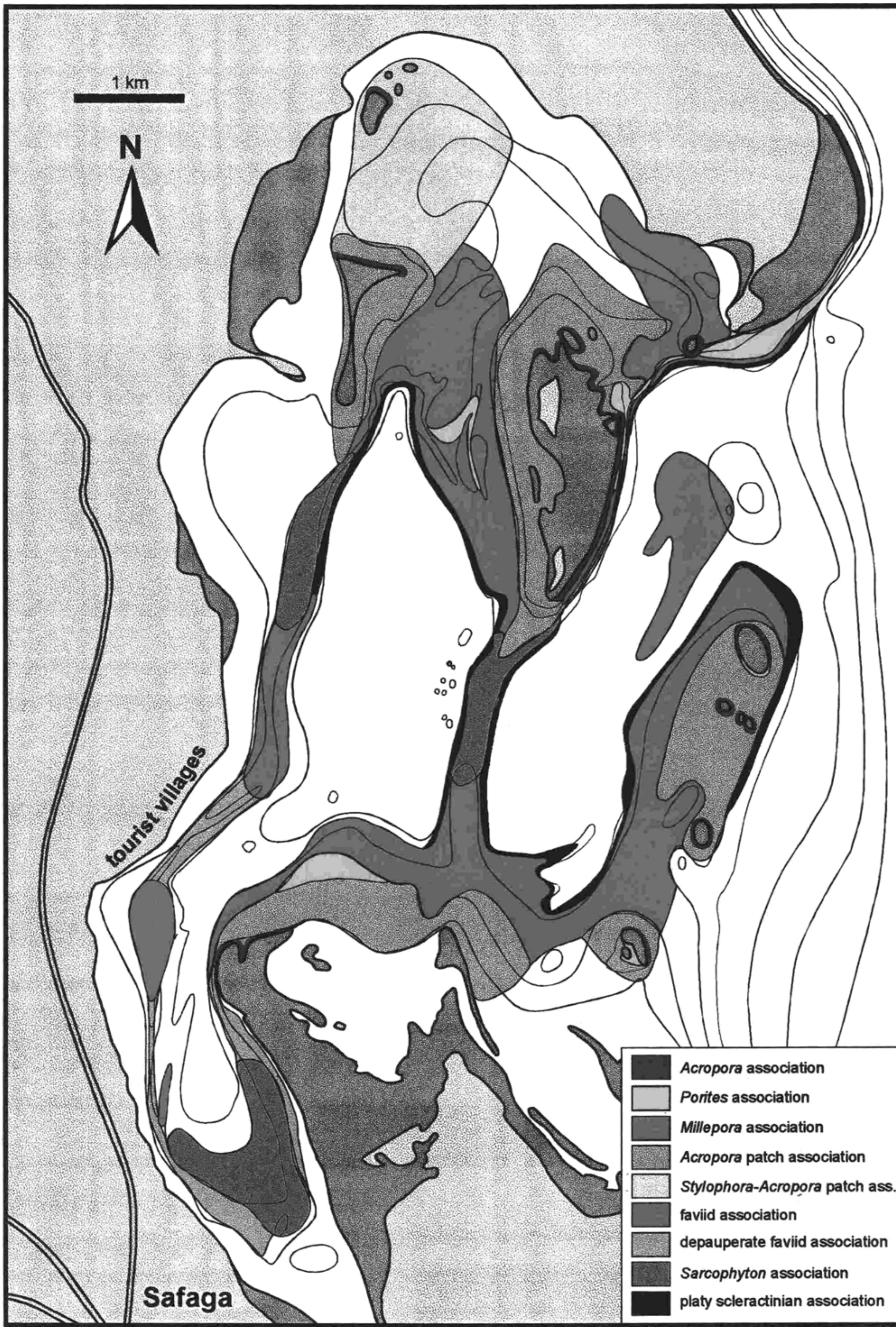


Fig. 2. Spatial distribution of coral assemblages in northern Safaga Bay. Stippled light grey areas are land, stippled dark grey areas are tidal flats.

	exposed	semi-exposed	sheltered
reef crest	*Stylophora pistillata*	*Stylophora pistillata*	*Stylophora pistillata* Faviidae
reef edge	*A. hyacinthus*-group	*Millepora dichotoma*	*Porites lutea*
reef slope	various *Acropora*, diverse without clear dominance	*Millepora dichotoma*	*Porites lutea* and others
slope base	tabular *Acropora*	*Acropora hemprichi*	tabular *Acropora* (*A. clathrata*, *A. divaricata*)
fore reef	diverse carpet	diverse carpet	not mentioned

Table 1. Basic reef differentiation (columns) and zonation (rows) with dominant coral taxa on reefs in the northern Red Sea (Gubal saghir island to Abu Hashish island) as described by RIEGL & VELIMIROV (1994). This zonation is basically used in this paper for the identification of coral assemblages.

the areal extent of the study, but to proceed with mapping coral assemblage distribution within the entire northern Safaga Bay by identifying coral assemblages visually. This allowed us to cover much more space than a fully quantitative approach.

Space partitioning of living benthos and substratum was estimated visually, and the dominant coral species were identified. Identification of corals followed SCHEER & PILLAI (1984), VERON & PICHON (1976, 1982), VERON et al. (1977), VERON & WALLACE (1984), VERON (1986), SHEPPARD & SHEPPARD (1991), and RIEGL (1995 a).

We use the term assemblage instead of community, as the assignment to different assemblages is qualitative. We reserve the use of the term community for quantitative descriptions. The definition of coral community sensu GEISTER (1983) for a loose assemblage of corals without frame building should be avoided, as it is in conflict with the biological usage of this term (MERGNER & SCHUHMACHER, 1981; DONE, 1982; RIEGL & VELIMIROV, 1994). The term assemblage is habitat independent and process neutral and makes no assumptions about ecological interactions between constituent species.

3 RESULTS

Most coral assemblages in northern Safaga Bay are clearly dominated by Scleractinia, with the exception of one assemblage type, which is dominated by the alcyonacean *Sarcophyton*. In some coral sub-assemblages Xeniidae actually covered more space than Scleractinia. But this soft-coral dominance was usually superimposed on a typical scleractinian assemblage.

The previous analyses of RIEGL (1989), KLEEMANN (1992) and RIEGL & VELIMIROV (1994) suggest a scleractinian species richness of well over 100 or roughly 80% of the total northern Red Sea scleractinian fauna as given in SHEPPARD & SHEPPARD (1991). Alcyonacea were not investigated in great detail, but were abundant.

Depending on bottom topography, two main coral-dominated systems are developed: true reefs with strong energy gradients and/or steep topographic relief, coral carpets (HOTTINGER, 1977; REISS & HOTTINGER, 1984; PILLER & PERVESLER, 1989) with low energy gradients and/or low topographic relief. The respective coral assemblages differentiate themselves along a depth gradient, a gradient of turbidity and sedimentation, and along a windward-leeward gradient.

3.1 Strong gradient and/or steep relief assemblages

3.1.1 The windward *Acropora* assemblage

This assemblage was described by RIEGL (1989) and RIEGL & VELIMIROV (1994) from the localities Shaab el Erg and Shaab Dhofar (spelled more correctly as Shaab Dorfa

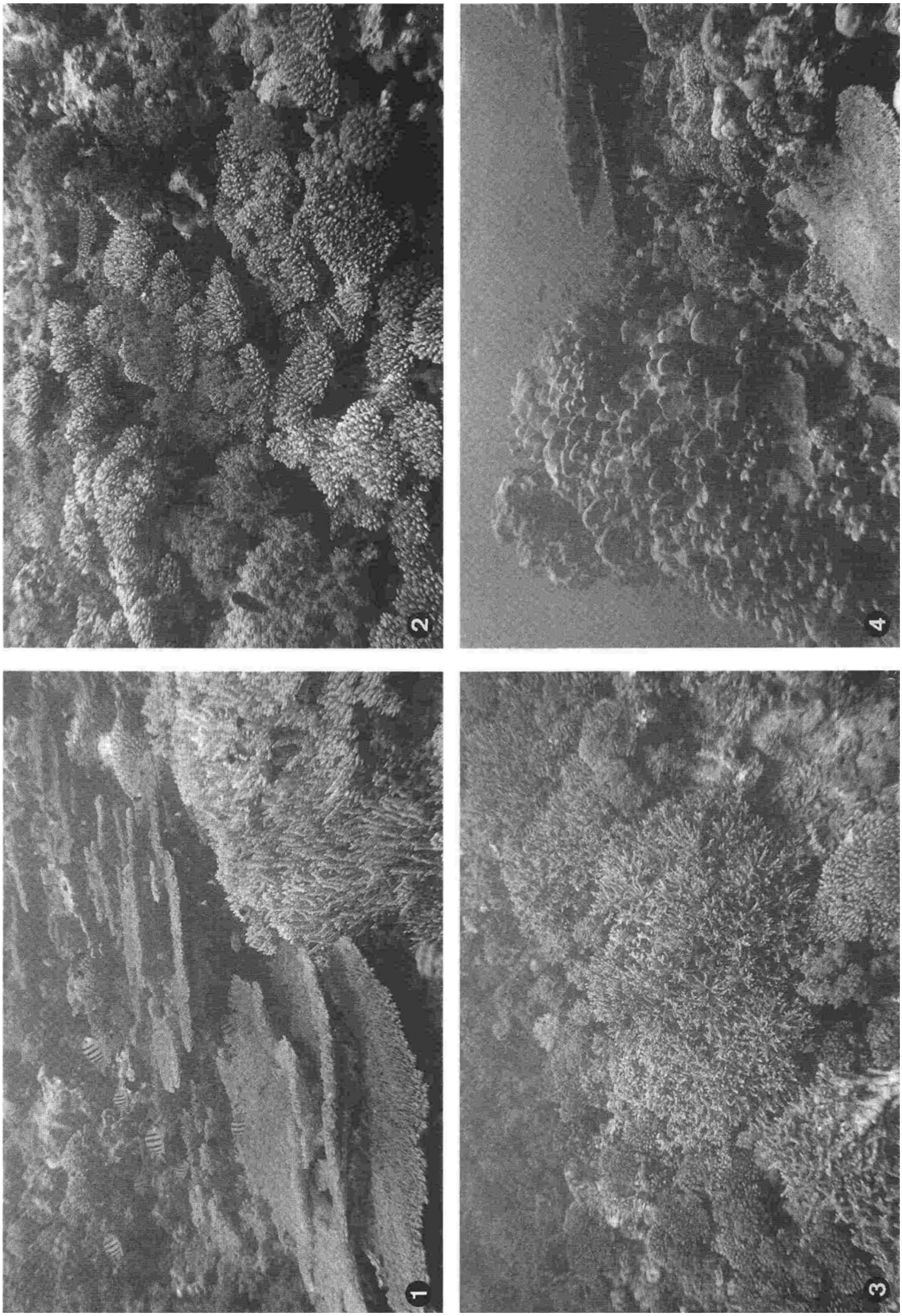
Plate 38 The windward *Acropora* assemblage in northern Safaga Bay.

Fig. 1. Upper reef slope of Tubya al-Kabir between 2 and 5 m depth. The tabular corals are *A. cytherea* and *A. hyacinthus*. The branching corals are *A. secale*.

Fig. 2. The same reef slope between 5 and 7 m depth. The small corymbose colonies are mostly *A. polystoma* with some *Pocillopora verrucosa*. The soft coral on the extreme left is a *Sinularia*.

Fig. 3. The same reef slope between 10 and 12 m depth. The large corymbose colonies in the centre are *Acropora hemprichi*, surrounded by smaller *A. polystoma* and *A. humilis*.

Fig. 4. *Hydnophora exaesa* is frequently found within the *Acropora* zones on exposed reef slopes (E Tubya al-Kabir).



in RIEGL, 1989) in the Giftun islands off Hurghada. A similar assemblage from Safaga Bay was described by KLEEMANN (1992) and by HEAD (1987) from the central Red Sea (Sudan). Within Safaga Bay it is found on windward, exposed reef edges and slopes (Fig. 2). The variable degree of wave exposure changes coverage by this assemblage: in areas of higher wave energies the entire reef slope and a large portion of the reef flat are covered, while in lower energy areas only a relatively narrow zone on the reef edge and uppermost reef slope (to about 2 m depth) as well as on the most seaward parts of the reef crest (up to 5 m) are included. It is an assemblage of high coral coverage, usually between 60 and 80 %.

The reef edge

The dominant and most characteristic coral on the actual reef edge is *A. gemmifera*, which also dominates on the reef flats immediately adjacent to the reef edge. This species appears to have a higher tolerance to exposure to air during extremely low tides as well as to waves breaking directly onto the colonies. Immediately below this narrow zone, from 1.5 m depth, tabular *Acropora* of the *A. hyacinthus* group (sensu VERON & WALLACE, 1984) are characteristic (Pl. 38/1). The most exposed parts are typically *A. hyacinthus* dominated (Straits of Gubal, RIEGL & VELIMIROV, 1994). However, in the more sheltered Safaga Bay, *A. cytherea* and *A. anthocercis* are also characteristic (windward edges of Tubya al-Kabir, Tubya al-Saghira, Gamul al-Kabir, Gamul al-Saghira, the NE facing fringing reef of Tubya al-Hamra and the fringing reef N of Gazirat Safaga). The tables are usually directed in such a manner, that they avoid the direct impact of breaking waves. As they are situated in the position where waves start shoaling and strong currents are induced, most colonies are highly calcified and show frequent anastomoses of horizontal branches which, in extreme cases, leads to the formation of plates. In slightly less exposed areas (NW facing fringing reef of Tubya al-Hamra, E facing fringing reef of Tubya al-Bayda) *A. anthocercis* takes the place of *A. hyacinthus*. Furthermore dense thickets of *A. secale* (Pl. 38/1) are found and numerous other *Acropora* species (*A. polystoma*, *A. tenuis*, *A. humilis*) form small, corymbose tables (ESE facing fringing reef of Tubya al-Bayda, E to ESE facing edges of Tubya al-Kabir and al-Saghira as well as Gamul al-Kabir and al-Saghira).

A special case of soft coral dominance by *Litophyton arboreum* on an exposed reef edge was observed on Tubya al-Saghira. We suppose that a denuded area was settled by the soft corals, which later competitively excluded *Acropora* recruits.

The reef slope

Particularly on the exposed offshore reefs Tubya al-Kabir and al-Saghira as well as Gamul al-Kabir and al-Saghira, the entire reef slope (which stretches to a depth of about 15 m) is characterized by an *Acropora* dominated assemblage (Pl. 38/2, 3). Coral coverage is mostly above 60 %. Below the *A. hyacinthus* edge follows a wide zone of corymbose tables with interspersed caespitose colonies. The characteristic species are *A. polystoma* (corymbose), *A. secale* (caespitose), and *A. humilis* (corymbose) (Pl. 38/2). From about 5 m downward, individual large tables of *A. divaricata* and *A. clathrata* are found. Between the *Acropora*, a diverse coral assemblage is found, consisting of most coral families (typical species are *Goniastrea retiformis* and *edwardsi*, *Psammocora haimeana*, *Echinopora hirsutissima*, *Gardineroseris planulata*). *Porites* colonies of variable size are common and typical for this type of assemblage. Large columnar colonies of *Pavona maldivensis* and *Hydnophora exaesa* are found (Pl. 38/4). The latter prefers the upper reef slope, the former the middle to lower reef slope.

On the lower reef slope and its base is a clearly defined *A. hemprichi* zone, represented by thickets which can attain several metres in diameter (Pl. 38/3). Big *A. hemprichi* thickets are found all over the reef slope, but dominate the assemblage only at depths greater than 10 m. Tabular *Acropora* species are *A. clathrata* and *A. divaricata*. Xeniidae are common and can make up as much as 50 % of the fauna. Space cover is up to 80 %.

The *Acropora hemprichi* zone was described from sheltered reefs in RIEGL & VELIMIROV (1994), while the base of exposed and semi-exposed reefs was described as having an *A. valida* zone. RIEGL (1989), however, describes the base of the reef slopes at Shaab el Erg, Shaab Dorfa (Shaab Dhofar in RIEGL & VELIMIROV, 1994), Abu Hashish, and Giftun saghir to be dominated by *A. hemprichi* among others (*A. humilis* and *A. valida*). We can therefore accept a more or less clearly defined *A. hemprichi* zone at the base of reef slopes in most exposures.

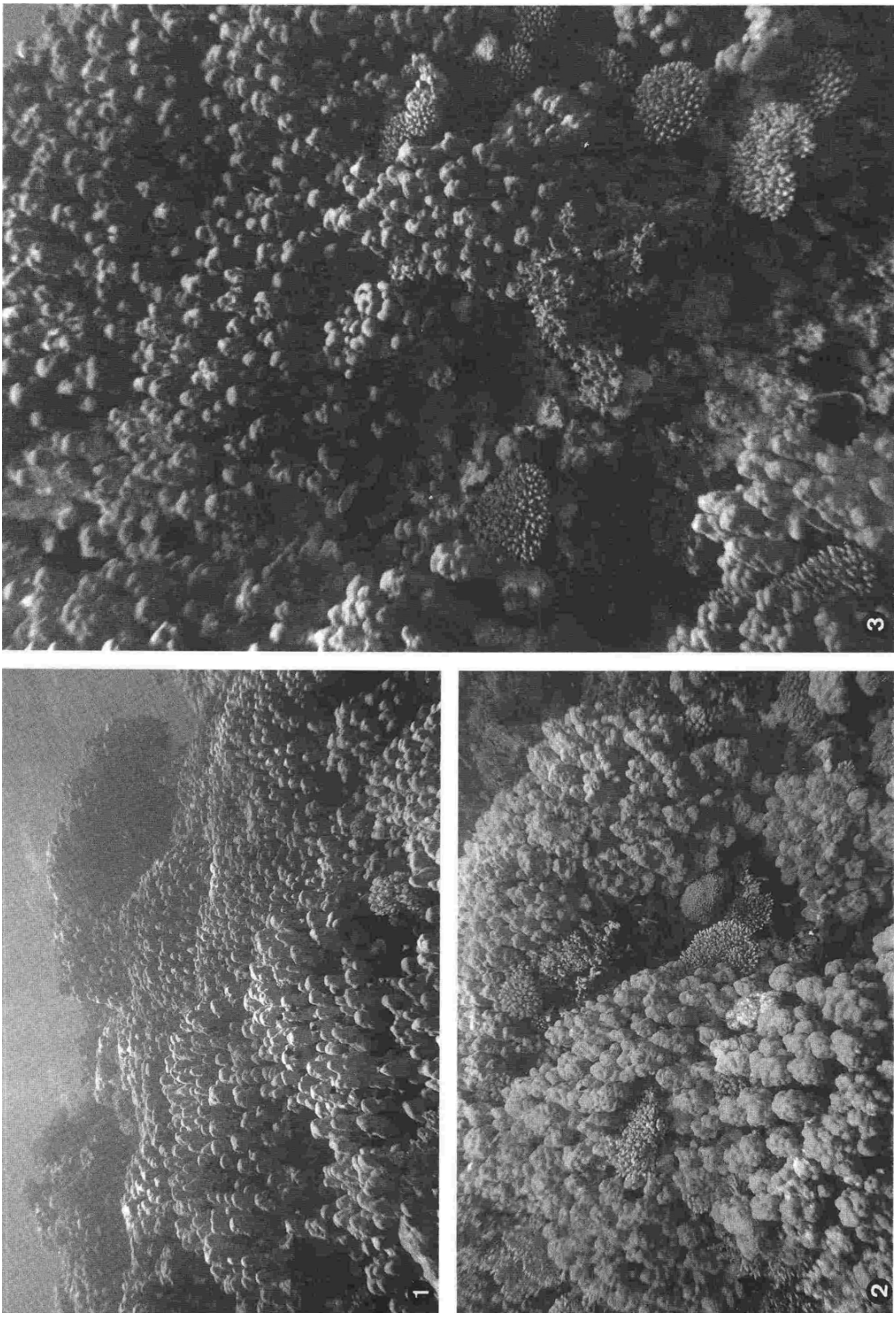
Most reef slopes end rather abruptly with the *Acropora hemprichi* zone and meet a flat sandy plain with numerous coral patches (except off Ras Abu Soma where the steep slope continues downwards) which are made up by a

Plate 39 The leeward *Porites* assemblage in northern Safaga Bay.

Fig. 1. Overview of the leeward slope of Tubya al-Kabir, made up entirely by *Porites lutea* colonies.

Fig. 2. The thick columnar growth form of *Porites lutea*. Other corals in this photo are *Acropora valida* (centre), *Acropora polystoma* (left), *Echinopora gemmacea* (centre), and *Pocillopora verrucosa* (top).

Fig. 3. Part of the reef slope of Tubya al-Kabir which is made up entirely by a single, big *Porites lutea* colony. *Acropora valida* has settled on the dead, lower parts of the colony.



diverse coral assemblage composed of mainly faviids and siderastreids but without any specific dominance. Characteristic are *Acropora* tables or arborescent colonies (typically *A. pharaonis*), which are found on almost every patch. Also *A. clathrata* is frequent in the upper parts of the patch zone, but disappears in depths greater than 15 m. Space cover of corals on the patches is around 25-50 % (compare 3.2.1).

3.1.2 The leeward *Porites* assemblage

This assemblage was described by Riegl (1989) and Riegl & Velimirov (1994) from the localities Giftun saghir and Shaab Abu Rimathi off Hurghada. The same coral assemblage is found in Safaga Bay (Kleemann, 1992) on leeward, although well flushed reef slopes, particularly on off-shore reefs (Tubya al-Kabir and al-Saghira as well as Gamul al-Kabir and al-Saghira). It is an assemblage of high coral coverage, usually between 80 and 100%, but relatively low diversity.

The reef edge

Depending on exposure, the reef edge may be developed in form of a '*Porites* ridge' (Head, 1987), which is made up entirely of *Porites* species, typically *P. lutea*. The reef edge *Porites* are the uppermost extension of colonies which often make up or cover much of the reef slope. Living coverage is high, often showing no interruptions over several metres, as adjacent *Porites* colonies fuse to form one solid ridge.

In more exposed areas, the reef edge can be dominated by a mixture of columnar *Pavona maldivensis*, *Hydnophora exaesa* or *Favia stelligera* interspersed with small *Acropora* spp. The more exposed the situation, the more *Acropora* becomes abundant.

The reef slope

The leeward reef slopes on Tubya al-Kabir and al-Saghira are entirely *Porites* dominated (Pl. 39/1-3). The typical species is *Porites lutea* of which big colonies, often of more than 5 m diameter, build up the reef slope. Only where disturbances have created gaps in the *Porites* colonies, are other corals found. Adjacent *Porites* colonies often merge to form "super-colonies" (Pl. 39/1).

Particularly towards the base of the reef slope other coral species increase in abundance and frequently tabular *Acropora clathrata*, *A. divaricata* and *A. pharaonis* are found. The tabular *Acropora* zone was also described in Riegl & Velimirov (1994, p.224) from Giftun saghir and Shaab Abu Rimathi, but *A. clathrata* was misidentified as *A. hyacinthus* (p. 224, Fig. 6b).

As *Porites* reef slopes are usually made up by a few giant colonies, they are relatively steep and an abrupt transition into the fore reef area is observed. Alternatively, the reef slope framework can gradually merge into a carpet, dominated either also by *Porites* or by faviids (e.g., at Tubya al-Hamra, SE Ras Abu Soma). These assemblages are described below.

3.1.3 The *Millepora* reefs

This is an assemblage primarily defined by the abundance of *Millepora dichotoma*. Riegl & Velimirov (1994) called this assemblage "semi-exposed" but a better definition would be "current exposed". Such reefs are subjected to relatively little direct wave action, but strong currents. In northern Safaga Bay, this assemblage is found on the E facing fringing reef of Tubya al-Bayda. This part of the fringing reef is oriented (sub)parallel to the dominant wind, wave and swell direction. Oncoming waves are therefore not stopped by the reef, but translated into a longshore current usually flowing in a southerly direction (Piller & Pervesler, 1989).

Depending on wave exposure, other elements can play an important role. This assemblage was originally described from Sal Hashish Island (Abu Hashish in Riegl, 1989) and Gubal saghir Island (Riegl & Velimirov, 1994). On Sal Hashish Island, a *Millepora dichotoma* dominance is superimposed on a coral assemblage characterized by a high frequency of *Porites*. This identifies the reef as being at the sheltered end of the semi-exposed scale. The Tubya al-Bayda fringing reef is a more typical *Millepora* reef, as the reef slope is more or less entirely dominated by *M. dichotoma*. Less developed examples occur at Ras Abu Soma at a small fringing reef on the bay side of the Ras and at small coral patches along the northern tip of Gazirat Safaga.

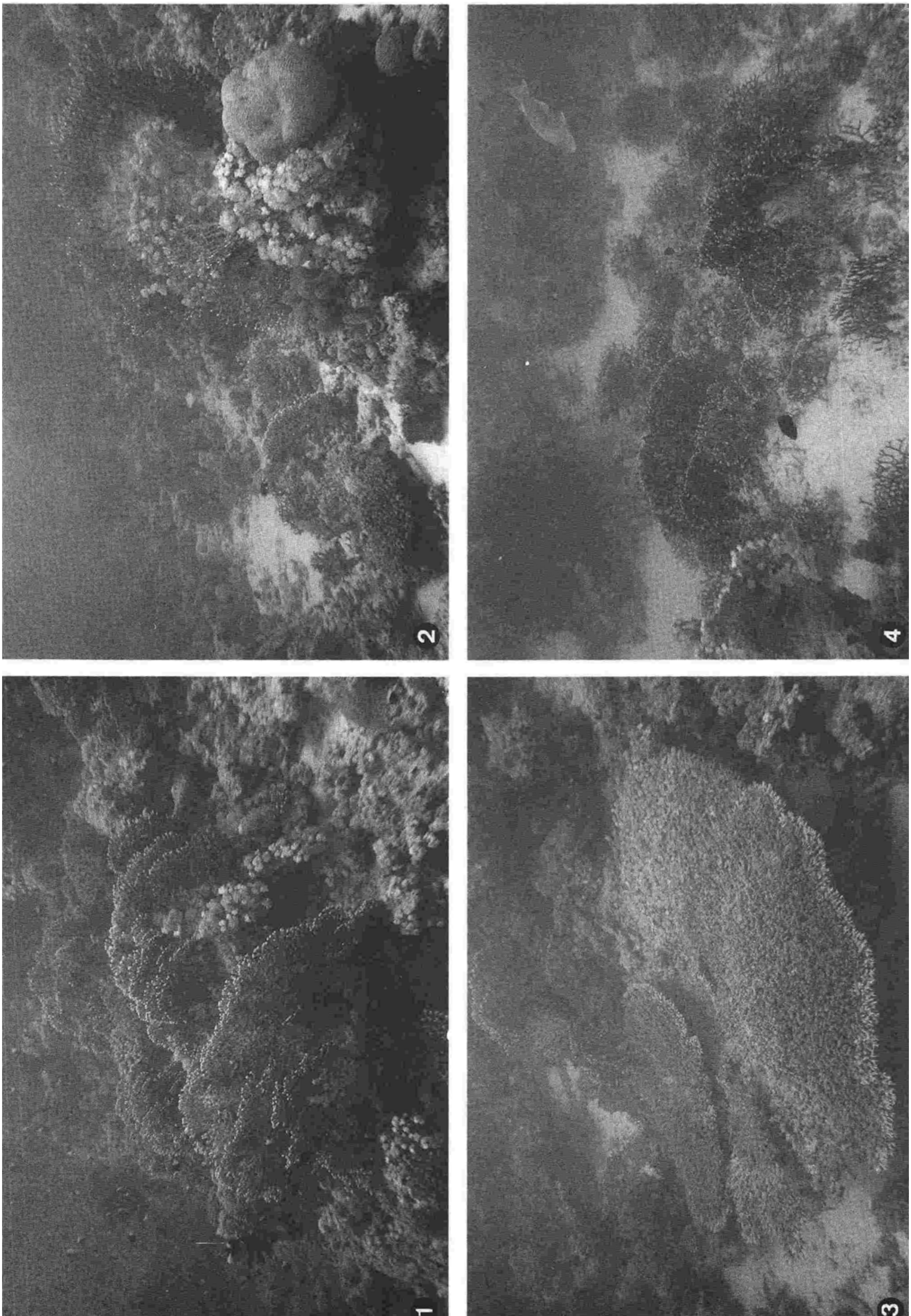
The reef edge

Depending on local topography, the reef edge shows more exposed *Acropora* dominated parts or more sheltered *Porites* dominated corners. In some areas, local soft coral dominance by *Litophyton arboreum* and *Sinularia* cf. *leptoclados* is observed. However, *Millepora* is always common on the reef edge. The most common species are *M. dichotoma* and *M. platyphylla*.

Other common corals are *A. gemmifera*, *A. secale*, and *Pocillopora verrucosa*. Space cover is usually high (30-70 %).

Plate 40 The *Millepora* assemblage in northern Safaga Bay.

Fig. 1. Reef slope at Tubya al-Bayda (5 m depth).
Fig. 2. Lower reef slope at Tubya al-Bayda with *Platygyra lamellina* and numerous xeniids.
Fig. 3. *Acropora clathrata* at the base of the reef slope/upper fore reef area (Tubya al-Bayda).
Fig. 4. Upper fore reef area at Tubya al-Bayda (12 m depth).



The reef slope

On a typical current exposed reef it is dominated by *Millepora dichotoma*, which makes up about 50% of all coral colonies on Tubya al-Bayda (Pl. 40/1, 2, 4). Other common species are *Acropora humilis* and *A. polystoma*, which form small corymbose tables. In between grow numerous small faviid, poritid and siderastreid colonies (Pl. 40/2). Among soft corals, xeniids are common, particularly on the lower reef slope. Space cover is around 50 %.

At the base of the reef slope, between 10 and 20 m, a zone of big (diameter up to 3 m) tabular *A. clathrata*, *A. pharaonis* and *A. divaricata* is found (Pl. 40/3). This zone continues into the fore-reef area. It is equivalent to the deep, tabular *Acropora* zone of Riegl & Velimirov (1994) mentioned above (3.1.2). This assemblage, as a deeper water assemblage, is found in most localities.

On Tubya al-Bayda a steep, sandy continuation of the rocky reef slope with numerous coral patches occurs. These patches are dominated by the big tabular *Acropora* species, which also dominate the lowermost reef slope (*A. clathrata*, *A. pharaonis*, *A. divaricata*). A diverse faviid assemblage is found on the rest of the patches. Coral cover is around 25 %.

3.1.4 The reef flat *Stylophora* assemblage

This assemblage is found on all shallow inter- and infratidal hardgrounds. It is a depauperate assemblage made up of a few hardy coral species, which are able to survive this harsh environment. Regular low tides, which expose much of the reef flats to air for several hours limit coral growth to regions where moisture is provided by splashing due to wave action or in depressions which form pools.

The typical corals close to the reef edge are *Acropora gemmifera*, *A. digitifera*, and *Pocillopora damicornis*. Landward of this narrow (up to 5 m wide) zone, the dominant coral is *Stylophora pistillata*. In depressions, *Porites lutea* and *P. solida* form small colonies. In some areas dense beds of the soft corals *Sinularia* or *Sarcophyton* can be found, which is similar to the situation described by Benayahu & Loya (1977) from the Sinai.

3.2 Low gradient and /or low relief assemblages

3.2.1 The *Acropora* dominated coral patches

Within this assemblage, *Acropora* dominates in an otherwise diverse assemblage of faviids. It is observed on exposed to well washed areas <20 m where topographical highs are formed or covered by coral knolls. *Acropora* species either dominate the entire patch or are concentrated at the periphery. The typical species are arborescent *A. hemprichi* and *A. horrida* as well as tabular *A. pharaonis*, *A. robusta*, *A. humilis*, and *A. tenuis*. Tabular colonies of these species are typically found on the periphery or the lower parts of the patches. *A. anthocercis* or *A. cytherea* sometimes cover the most apical parts of shallow patches. Such an assemblage is found north of Tubya al-Hamra, E of al-Dahira, N of Gazirat Safaga and on the shallow submarine plain stretching from Tubya al-Kabir to Gamul al-Kabir.

In areas influenced by strong currents, like some areas north of Tubya al-Hamra, the most apical parts of the reef patches are occupied by *Millepora dichotoma*, a rheophilic indicator (Mergner, 1977; Riegl & Velimirov, 1994).

3.2.2 The *Stylophora-Acropora* coral patch assemblage

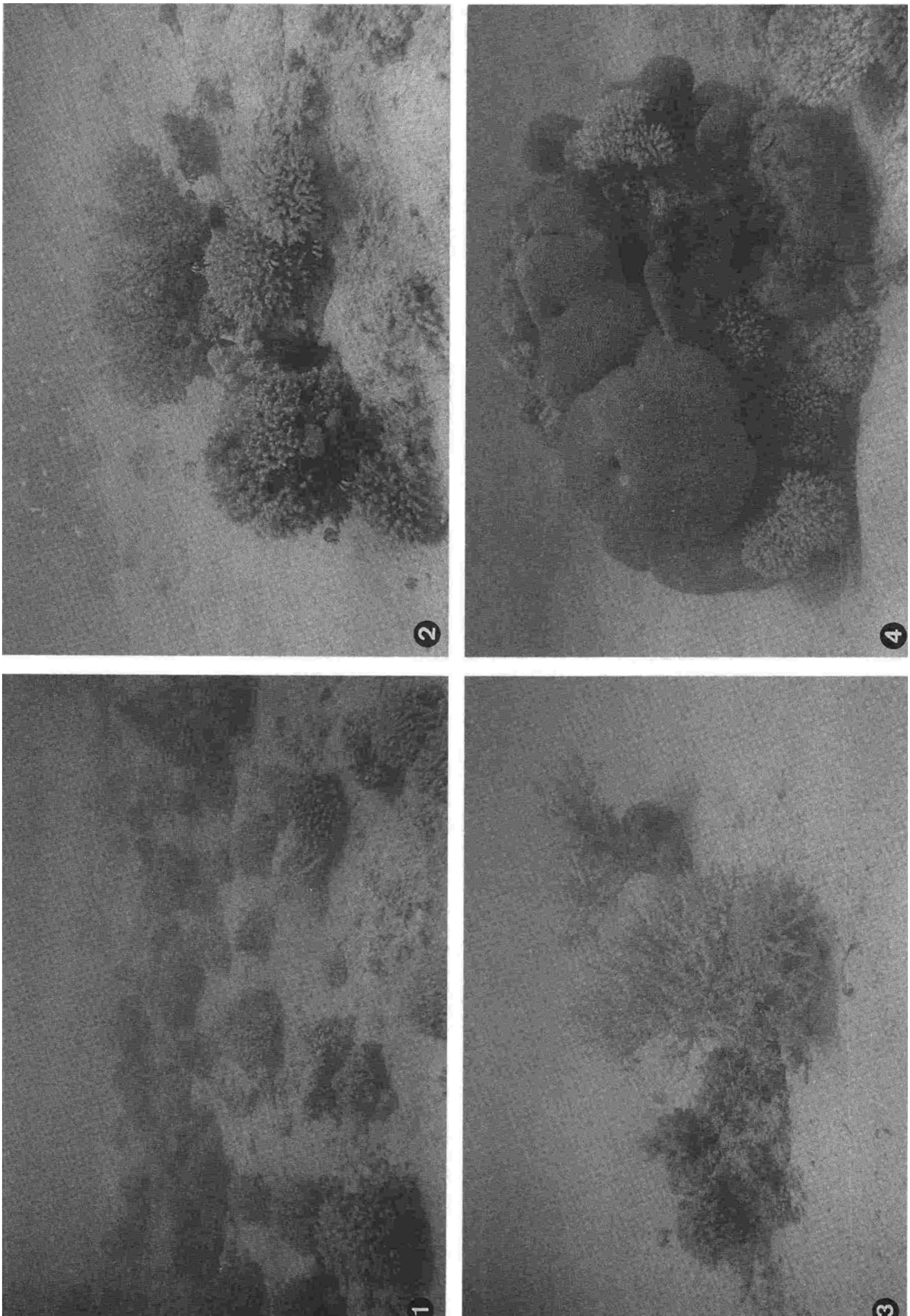
This assemblage is found in shallow areas in the northernmost part of Safaga Bay (Fig. 2), where fossil limestone substrate is covered by a sediment layer of varying thickness. Wherever sufficient hard substratum is available, individual coral heads have settled or small coral patches have developed. The characteristic coral of this area is *Stylophora pistillata*, which forms dense bushy colonies usually about 50 cm in diameter (Pl. 41/1). *Acropora robusta*, *A. tenuis*, *A. pharaonis*, and *A. anthocercis* form large corymbose or tabular colonies (Pl. 41/2, 3). The bases of these colonies are usually densely packed with xeniids. Characteristic massive corals are *Platygyra lamellina* and *Porites lutea* and *solida*, which can form big microatolls up to several metres in size (Pl. 41/4). Often these microatolls form clusters, which then provide a habitat for other corals and represent very shallow patch reefs. Common soft corals are *Litophyton arboreum* and Xeniidae, which settle on debris or gravel. These colonies then appear to be free-living in the sand, but, in the case of *L. arboreum*, are always attached to a larger (several cm in size) piece of debris (usually a broken coral) which can, however, be buried several cm under the sand. Small *Xenia* colonies are often only attached to pebbles. They frequently outgrow their foothold and then live virtually unattached in the sand. On microatolls, the Alcyoniidae *Sarcophyton* spp. and *Lobophytum* cf. *venustum* are often encountered.

3.2.3 The *Porites* carpet

Although this assemblage was encountered in the sample area off Hurghada, it was not described in Riegl (1989)

Plate 41 The *Stylophora/Acropora* coral patch assemblage in northern Safaga Bay.

Fig. 1. Almost monospecific stand of *Stylophora pistillata* at 2 m depth north of al-Dahira.
Fig. 2. *Stylophora pistillata* and *Acropora tenuis* in 3 m depth north of al-Dahira.
Fig. 3. *Acropora pharaonis* and *Stylophora pistillata* at 5 m depth north of al-Dahira.
Fig. 4. *Platygyra lamellina* and *Stylophora pistillata* in 2 m depth north of al-Dahira.



and RIEGL & VELIMIROV (1994). The typical depth distribution of this assemblage is between 5 and 15 m. It shows a restricted distribution within northern Safaga Bay: a continuous belt stretching from Ras Abu Soma to the southern tip of Tubya al-Hamra, a patch between Tubya al-Hamra and al-Dahira, and a larger patch NW of Gazirat Safaga (Fig. 2). It is found in areas of low topographical relief, primarily in shallow areas.

As the name implies, the *Porites* carpet is clearly defined by the overwhelming importance of *Porites* species, the most important are *P. columnaris* and *P. lutea* (Pl. 42/1-4). The typical growth form is columnar in both species (contrary to the sometimes fully massive colonies of *P. lutea* on reef slopes). Also *Porites (Synaraea) rus* is common, but not as important as the former two *Porites* species.

The *Porites* carpet is an area of vigorous frame-building (sensu GEISTER, 1983), the thickness of the clearly *Porites* built frame often exceeds 2 or even 3 metres (thickness at Ras Abu Soma between 2 and 3 m, between Tubya al-Hamra and al-Dahira 1 - 2 m, NW of Gazirat Safaga 2 - 3 m). The framework is characterized by numerous caverns between the stick-like *Porites* columns, which are usually only alive at their tips. This also gives rise to high coral diversity, as the dead parts of the *Porites* columns are settled by other corals (Pl. 42/2). Particularly encrusting and platy species (*Montipora* spp., *Echinophyllia aspera*, *Mycedium elephantotus*, *Echinopora lamellina*) are common, as are whorl-like *Turbinaria mesenterina* and small, corymbose *Acropora* (*A. valida*, *A. granulosa*, *A. humilis*). The abundance and diversity of faviids is relatively low, possibly due to the limited amount of space.

Soft corals are generally not important. In more current exposed localities, as Ras Abu Soma, numerous *Litophyton arboreum* occur. Xeniids are always common, although not as preponderant as in other deep assemblages, like the faviid carpet (see below).

The *Porites* carpet only occurs to a depth of 15 m, where it is replaced by a faviid carpet.

3.2.4 The faviid carpet

This is the most widely distributed coral assemblage in depths around and greater than 10 m (lower limit approx. 25 m) throughout northern Safaga Bay (Fig. 2). It has previously not been described to any great detail but was mentioned and illustrated as "coral carpet" in PILLER & PERVESLER (1989). RIEGL & VELIMIROV (1994) remark on "dense hard and soft coral carpets in the fore reef areas", but do not give any details due to insufficient sampling.

The coral assemblage of the faviid carpet is highly diverse, but clearly dominated by Scleractinia, usually members of the family Faviidae; the most characteristic species is *Goniastrea pectinata* (Pl. 43/1). This is an area of important carbonate accretion, the coral framework being on average 50-100 cm thick, but reaching to over 200 cm in extremely well developed areas, where individual large *Porites* colonies are found. The coral framework (sensu GEISTER, 1983) has a rugged surface topography, with individual coral colonies (*Goniastrea retiformis*, *G. pectinata*, *Platygyra lamellina*) forming columnar protrusions which overtop the rest of the carpet frequently by several tens of centimetres (Pl. 43/3).

The coral carpet is dissected by fissures, caves and gullies which are the habitat for a rich semi-cryptic to cryptic assemblage, including corals, sponges and ascidians (Pl. 43/2).

Typical corals in this assemblage belong to the genera *Favia*, *Favites*, *Leptastrea*, *Cyphastrea*, *Platygyra*, *Goniastrea*, *Pavona*, and *Echinopora* (Pl. 43/4). Among *Echinopora*, *E. lamellosa*, *E. horrida* and *E. gemmacea* are found in this assemblage, while *E. hirsutissima* is only common on exposed reef slopes. *E. gemmacea* occurs mainly in its branching *fruticulosa* form. In *Goniastrea*, *G. pectinata* is characteristic for this area, while *G. edwardsi* and *G. retiformis* favour exposed reef slopes. Large colonies (up to 3 m diameter) of *Lobophyllia corymbosa* are characteristic. Typical *Acropora* are *A. granulosa* and the rare *A. squarrosa*. Large tabular colonies are missing, the most frequent tabular species is *A. pharaonis*. Among other branching corals, *Pocillopora damicornis* is common, as is *Stylophora pistillata*. Free-living corals include big colonies of *Ctenactis echinata* and *Herpolitha limax*. *Merulina ampliata* is frequent, forming numerous short branches in this environment. Platy corals, such as *Turbinaria mesenterina*, *Echinophyllia aspera* and *Mycedium elephantotus* are common, particularly in deeper areas, where this assemblage intergrades with the deep platy scleractinian assemblage.

Soft corals, particularly Xeniidae are characteristic.

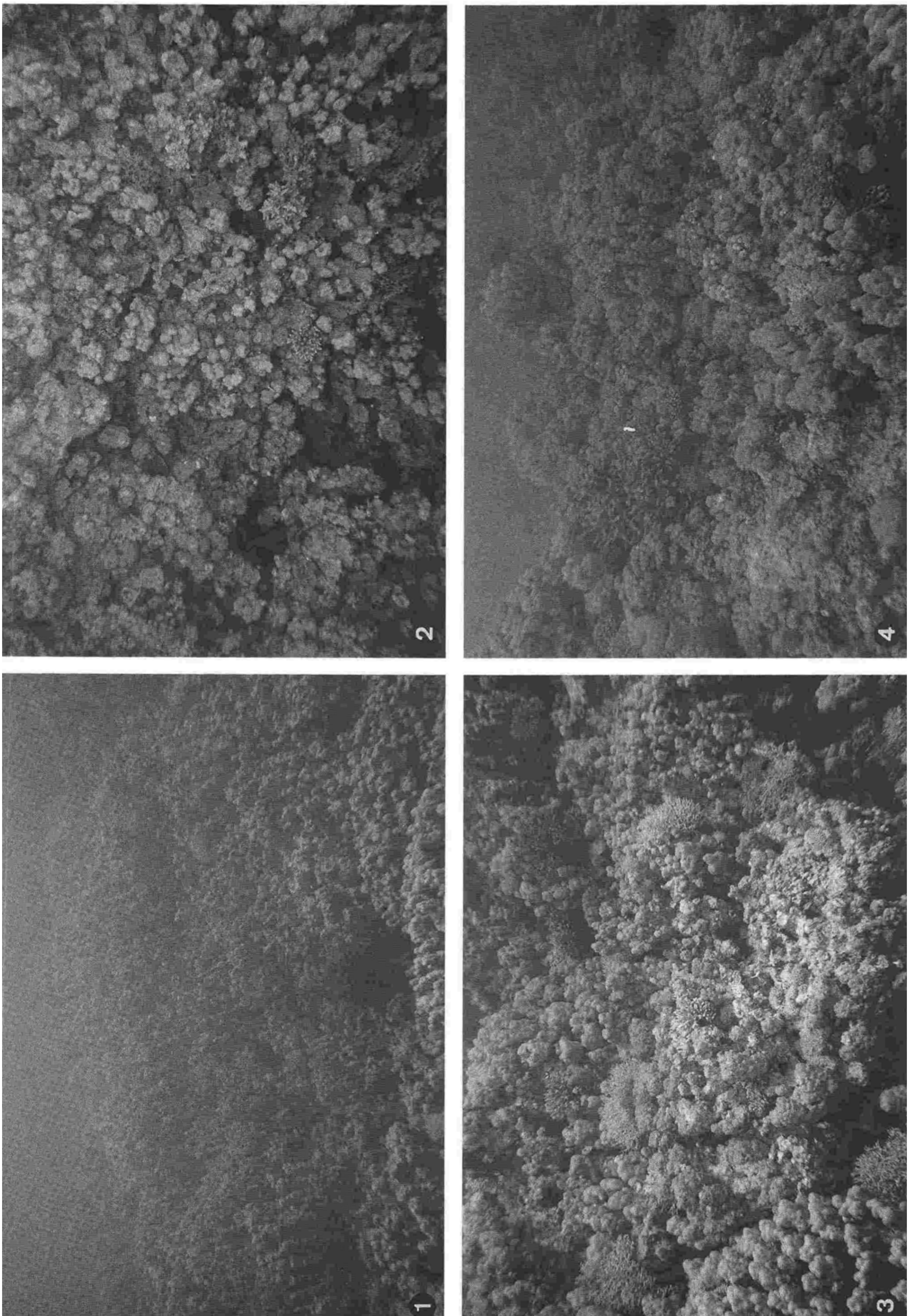
Plate 42 The *Porites* carpet in northern Safaga Bay.

Fig. 1. *Porites lutea* and *Porites columnaris* carpet west of Tubya al-Hamra, 6 m depth.

Fig. 2. *Porites columnaris* carpet. Only the tips of the columns are alive, the dead lower parts are substratum for other colonies such as *Acropora hemprichi* (lower right), *Acropora cerealis* (lower centre) and *Seriatopora hystrix* (bottom centre). West of Tubya al-Hamra, 8 m depth.

Fig. 3. *Porites lutea* (left) and *Porites columnaris* (right) carpet with numerous *Seriatopora hystrix*. West of Tubya al-Hamra, 7 m depth.

Fig. 4. *Porites lutea* carpet south of Ras Abu Soma, 6 m depth.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This area has the highest diversity of *Heteroxenia*. Of the Alcyoniidae, particularly *Sarcophyton* species are much in evidence. Xeniids can in places make up about 50 % of all colonies, although the average is much lower.

Diversity in this assemblage is high, the highest of all assemblage types in Safaga Bay. Space coverage is between 60 and 90 %.

The depauperate faviid assemblage

This assemblage is found on the landward side of western Safaga Bay particularly in the "Southwest channel" (Fig. 2).

Basically, this is a depauperate faviid carpet, where most sediment susceptible elements were eliminated. Living coral cover is reduced, never exceeding 50 %, usually less than 25 %, but often remaining below this level. The assemblage is dominated by massive, hemispherical species (e.g., *Favia* spp., *Favites* spp., *Coscinaraea monile*). Few branching species remain, the most common being the fruticulose growth form of *Echinopora gemmacea*, the most frequent *Acropora* is *A. pharaonis*. Other common species are *Cycloseris* sp.

3.2.5 The *Sarcophyton* carpet

This is an assemblage type which has not been previously described in this context. A similar assemblage is known from the Sinai (BENAYAHU & LOYA, 1977), but its occurrence in shallow water makes it different from the assemblage described here. The *Sarcophyton* carpet occurs typically in depths between 10 and 30 m. It is distributed in Safaga Bay on the ridge between Tubya al-Bayda and Gazirat Safaga, as well as on the western margin of the bay (Fig. 2).

The dominant and most characteristic coral species are *Sarcophyton* spp., particularly *Sarcophyton glaucum* (Pl. 44/1). They clearly dominate the assemblage in terms of abundance and space coverage. However, Scleractinia are also important assemblage members, the most typical being *Siderastrea savignyana* and *Astraeopora myriophthalma* (Pl. 44/3). Fungiids, particularly *Cycloseris* spp. and *Herpolitha limax* (Pl. 44/2) are more evident in this assemblage than in the others, which is possibly due to the relatively low coral coverage which makes these species more apparent. Scleractinia are usually small, averaging about 10 cm in diameter, with only individual colonies, particularly *A. myriophthalma*, reaching sizes of up to 50 cm. *Porites* and *Acropora* are rare. *P. mayeri* and *P. solida* frequently form small colonies, *A. granulosa* and *A. squarrosa* occur frequently but only scattered *A. pharaonis* or *A. horrida* occur around the upper depth limit (Pl. 44/4).

3.2.6 The platy scleractinian assemblage

This coral assemblage, which is widely distributed in northern Safaga Bay (Fig. 2), is a continuation of the faviid carpet from depths beyond 25 m and can be found with several variations of dominant species. As it is a low-light assemblage, platy growth-forms, which allow maximum light utilization are typical. It is mostly dominated by faviids, of which particularly *Oulophyllia crispa* and many *Favites* species tend to a flat, spread-out growth form. Truly platy species, such as *Pachyseris speciosa*, *Echinophyllia aspera*, *Mycedium elephantotus*, and, typically, *Leptoseris papyracea* as well as *L. yabei* are common (Pl. 45/1-4). Particularly in the deepest regions, between 35 and 45 m, *Leptoseris* is common and characteristic of this coral assemblage (Pl. 45/3-4). The platy scleractinian assemblage is best developed on steep slopes and small drop-offs (e.g., in the basin of the "West area", Fig. 2). Diversity is high due to the numerous small colonies. Soft corals are common, various Xeniidae make up around 50 % of all colonies. Living substratum cover is at around 30-50 %.

A similar assemblage was described by LOYA & SLOBODKIN (1971) and LOYA (1972) and illustrated by HOTTINGER (1977) and REISS & HOTTINGER (1984) from the deep fore reef region of Eilat in the Gulf of Aqaba.

4 DISCUSSION

The coral assemblages observed in Safaga Bay are comparable to those of other areas in the northern Red Sea (RIEGL, 1989; SHEPPARD & SHEPPARD, 1991; RIEGL & VELIMIROV, 1994), the Gulf of Aqaba (LOYA & SLOBODKIN, 1971; LOYA, 1972; MERGNER & SCHUHMACHER, 1974; HOTTINGER, 1977; REISS & HOTTINGER, 1984) and the central Red Sea (HEAD, 1987; MERGNER & SCHUHMACHER, 1985; SCHUHMACHER & MERGNER, 1985). It appears that a fairly stable spatial pattern exists in the distribution of coral assemblages, at least on reefs in the northern half of the Red Sea. The pattern of assemblages described for Safaga Bay is therefore also applicable in other areas in the northern Red Sea. According to SHEPPARD & SHEPPARD

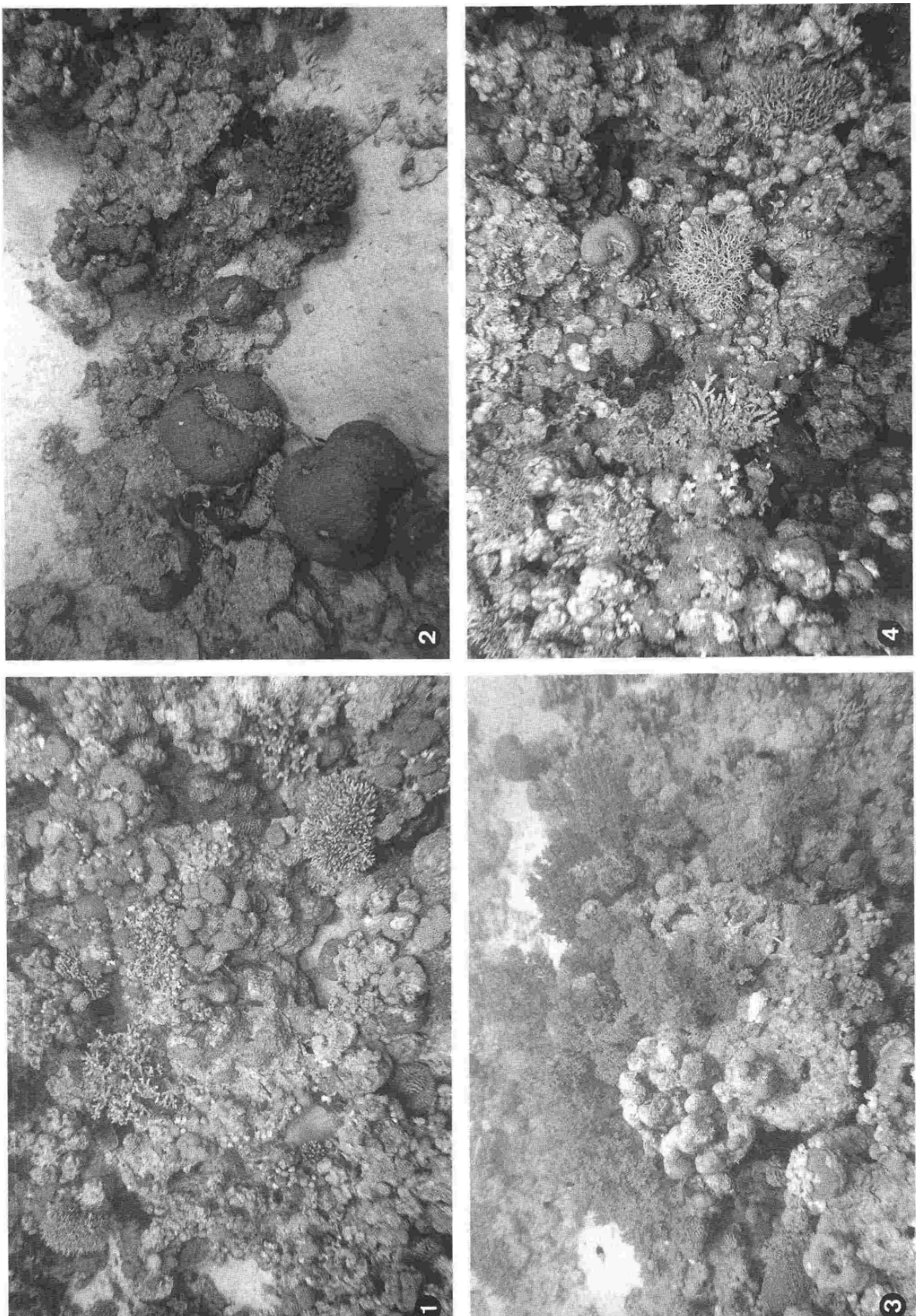
Plate 43 The Faviid carpet in northern Safaga Bay.

Fig. 1. Typical aspect with *Goniastrea pectinata* (centre), *Echinopora gemmacea* var. *fruticulosa* (centre left), various *Leptastrea* (centre right), *Platygyra lamellina* (right and bottom), *Acropora valida* (bottom right), and others. West of Tubya al-Hamra, 11 m depth.

Fig. 2. Sandy gullies within the Faviid carpet. The two big colonies are *Favites complanata*. In the centre are several small *Porites solida*. The bivalve *Tridacna maxima* is common within this assemblage. West of Tubya al-Hamra, 10 m depth.

Fig. 3. Faviid carpet with high frequency of the alcyonacean *Litophyton arboreum*, which is indicative of strong water movement. Tubya Arba, 15 m depth.

Fig. 4. Typical high diversity faviid carpet. N of Tubya al-Hamra, 12 m depth.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(1991) and SHEPPARD et al. (1992) coral communities in the southern Red Sea are different.

In areas of accentuated topography, the strong gradient and/or steep relief assemblages are found. The *Acropora* assemblages, particularly those on reef slopes, are primarily influenced by wave action as was apparent from long-term observation during all seasons. They grow in an environment of presumed maximum oxygen saturation and light availability which allows rapid growth. Therefore, the corals are capable of producing sturdy skeletons able to withstand the hydrodynamic forces, and fast repair growth can take place in the event of damage. All corals dominating in this environment have a highly organized, directional growth form which allows effective modification of basic morphology to suit the environment. Most are also efficient asexual reproducers (HIGHSMITH, 1982; RIEGL & VELIMIROV, 1994). Therefore, breakage in heavy seas is not necessarily a disadvantage to these species, which can regenerate from fragments. On the base of the reef slopes a "secondary zone" sensu MERGNER & SCHUHMACHER (1974) of *Acropora valida* was described by RIEGL & VELIMIROV (1994). The idea is that fragments (generated by storms or bioerosion) derived from the upper reef slope come to rest at the base of the reef slopes and regenerate there, which then leads to their dominance of the community. It is likely that the wide *Acropora* zones on exposed reef slopes are at least partly maintained by fragment regeneration on the lower slopes with strong input from populations on the upper slopes and edges. At the bases of the reef slopes, no rubble accumulations were observed which would have indicated that many fragments were washed off the reef. It is therefore assumed that wave action is generally not sufficient to cause widespread, catastrophic damage to windward *Acropora* communities, but that most fragments actually remain on the reef slope, where they can regenerate.

The *Porites* assemblage is found on leeward reef slopes which are not directly influenced by wave action. It is an assemblage dominated by massive, slow growing species forming huge colonies indicative of high age and therefore long-term stability of environmental conditions. This assemblage is a typical climax assemblage with low diversity and dominance of slow growing k-strategists. This leads to the intuitive assumption that these assemblages have been subjected to a low frequency of disturbances and that they have had enough time to replace the original r-selected set of species within the assemblage (PIANKA, 1970; CONNELL, 1978). This slow growing *Porites* species are competitively weak (THOMASON & BROWN, 1984) and achieve dominance through persistence rather than fast growth and aggressive behaviour. According to PÄTZOLD (1984) they are not subjected to equally strong seasonal variability in growth and mortalities under extreme temperature conditions like many other competing species (COLES & FADLALLAH, 1991). Coupled with their longevity, this allows them to dominate the coral community over long undisturbed time-spans (CONNELL, 1978). *Porites* are also capable of asexual propagation (HIGHSMITH, 1982) and particularly bigger colony parts can survive on sand thus generating new nuclei for further frame building.

The *Millepora* assemblage on current exposed reefs is situated somewhat half-way between the frequently disturbed windward assemblages and the rarely disturbed leeward assemblages. *Millepora dichotoma* has a wide ecological tolerance ("euryphot-rheophilic" indicator: RIEGL & VELIMIROV, 1994). This species generally avoids areas of high wave energy due to its fragile growth form but it is found in dense, frequently monospecific stands in current-exposed areas where its platy colonies are always oriented perpendicular to the dominant current direction (VELIMIROV, 1973; REISS & HOTTINGER, 1984). *Millepora* assemblages are mostly found on reefs growing along a N-S axis which thus do not experience direct impact of the dominant northwesterly or northeasterly swells. The sidewise impact of these swells creates constant currents along the reefs which benefit the *Millepora* community. Periodic disturbances by storms, however, are frequent enough to prevent complete dominance of this system by *Millepora*. *Millepora* dominance can vary from low on frequently disturbed reefs (tending towards an *Acropora* assemblage) to high on rarely disturbed current exposed reefs (almost total *Millepora* dominance with many *Porites* in sheltered localities).

The reef flat *Stylophora* assemblage in northern Safaga Bay is primarily influenced by low tides, which cause emergence of the reef flats and uppermost reef edges. This situation is common in the northern Red Sea (FISHELSON, 1973). *Stylophora pistillata* is a classical example of an r-strategist, which can dominate this area (LOYA, 1976 a,b,c). Besides their high resistance to desiccation, the numerous faviids are also able to tolerate sedimentation and, in addition, they have high tissue regenerative powers (FISHELSON, 1973). They only form small colonies within this system. The most important environmental factors acting on this assemblage are high temperature variability, recurrent desiccation during extremely low tides and resuspension of sediment in stormy conditions (FISHELSON, 1973; LOYA, 1976 c; MONTAGGIONI et al., 1986).

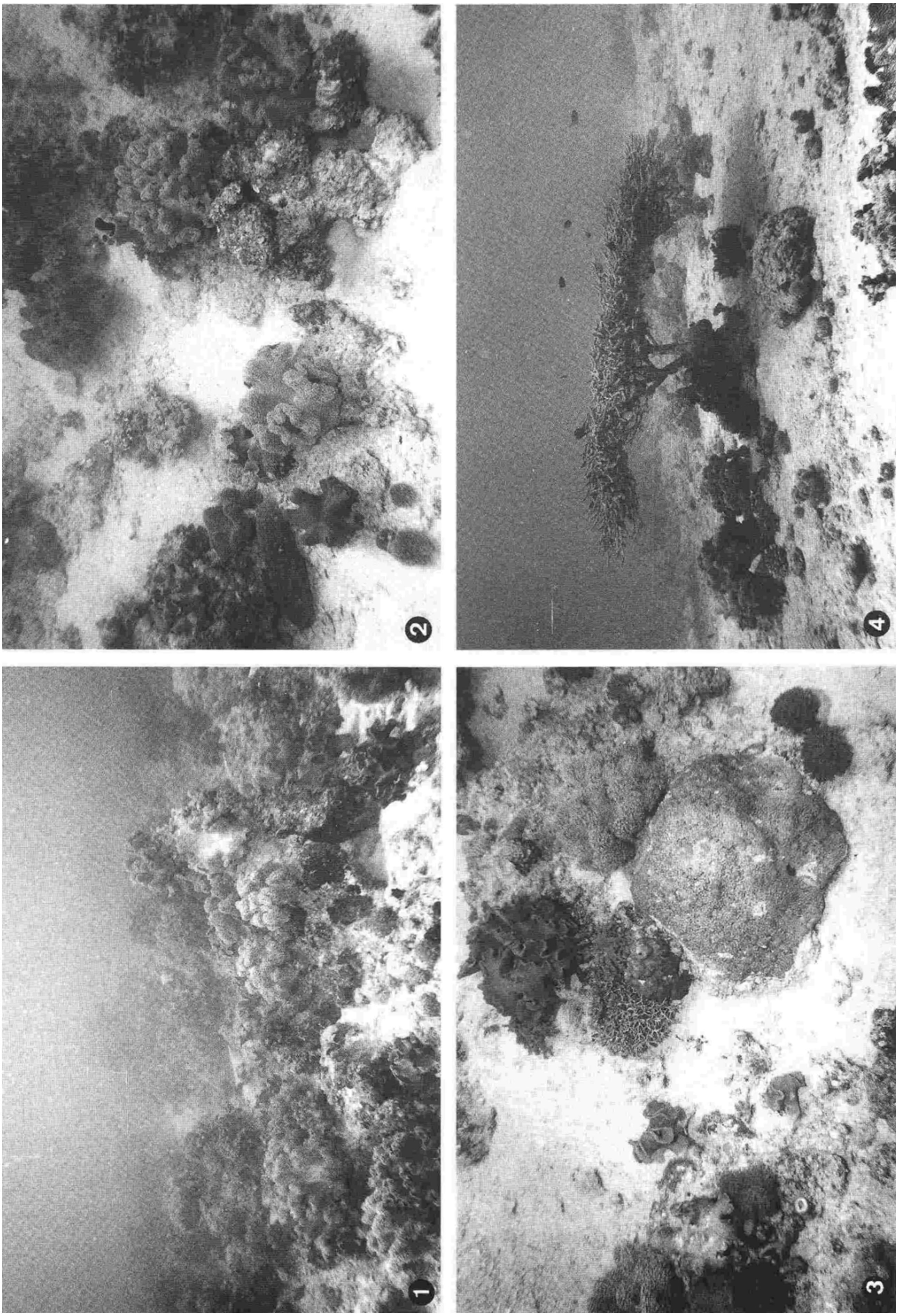
Plate 44 The *Sarcophyton* carpet in northern Safaga Bay.

Fig. 1. Typical aspect at 20 m south of al-Dahira.

Fig. 2. *Sarcophyton glaucum* with the fungiid *Herpolitha limax* (left). South of al-Dahira, 22 m depth.

Fig. 3. Typical scleractinia within the *Sarcophyton* carpet are *Astraeopora myriophthalma* (centre) and *Seriatopora hystrix* (centre left). South of al-Dahira, 16 m.

Fig. 4. A zone of tabular *Acropora pharaonis* is developed at the shallow end of the *Sarcophyton* carpet. South of al-Dahira, 12 m depth.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ROSEN (1975, 1981) and PERRIN et al (1995, p. 204) provided a model for the relationship of scleractinian coral communities in Indo-Pacific reefs to gradients of light energy and hydrodynamic exposure (Fig. 3). In this model, a faviid assemblage is reported to be found in areas of higher hydrodynamic exposure and in areas of higher irradiation than a *Porites* assemblage. Our results complement this model for the northern Red Sea and suggest that *Porites* assemblages can also be found both in areas of higher wave energy and light availability. This is inferred by the *Porites* dominance on sheltered upper reef slopes and the high frequency of small *Porites* colonies on exposed reef slopes (and the shallower position of the *Porites* carpet relative to the faviid carpet). Due to the lower hydrodynamic exposure of the northern Red Sea, the two most exposed communities of ROSEN (1975, 1981) are missing: the algal ridge and the *Pocillopora* community (Fig. 3). There is, however, the possibility that the assemblages described by ROSEN and us are not equivalent and that there may exist different types of faviid and poritid assemblages, which would be positioned differently in the model.

In areas of flat topography the low gradient and/or low relief assemblages were found. The *Stylophora*/*Acropora* coral patch assemblage often takes the aspect of a richer, more diverse reef flat and lagoon assemblage, with isolated *Acropora* (*A. pharaonis*, *A. robusta*) as well as big *Porites lutea* and *Platygyra lamellina* microatolls (see also MERGNER & SCHUHMACHER, 1974). It is influenced by similar environmental factors like the reef flat *Stylophora* assemblage. Within this assemblage a high frequency of *Sinularia* spp. was found, comparable to that observed by BENAYAHU & LOYA (1981) on shallow reefs in the Sinai. It is found in slightly deeper water (0.5-2 m) than the *Stylophora* assemblage and therefore in a somewhat more stable environment. In this region, variability in chemistry of the restricted and shallow water body as well as the sandy substratum covering rock bottom are the most likely reasons for the low diversity and overall living coverage of this coral assemblage.

The faviid carpet, as the most widespread assemblage type, is modified in response to changing environmental conditions (Fig. 3). If environmental quality declines it degrades into the depauperate faviid assemblage. If environmental quality increases, water is clear and plenty of light is available, *Porites* become increasingly common and the assemblage changes into a *Porites* carpet. Both assemblages (faviid and *Porites* carpets) are considered to be climax communities, resultant from long periods without any disturbances, as they are clearly dominated by k-strategists (PIANKA, 1970; CONNELL, 1978). Geologically, they are the most important assemblages due to their high frame building potential.

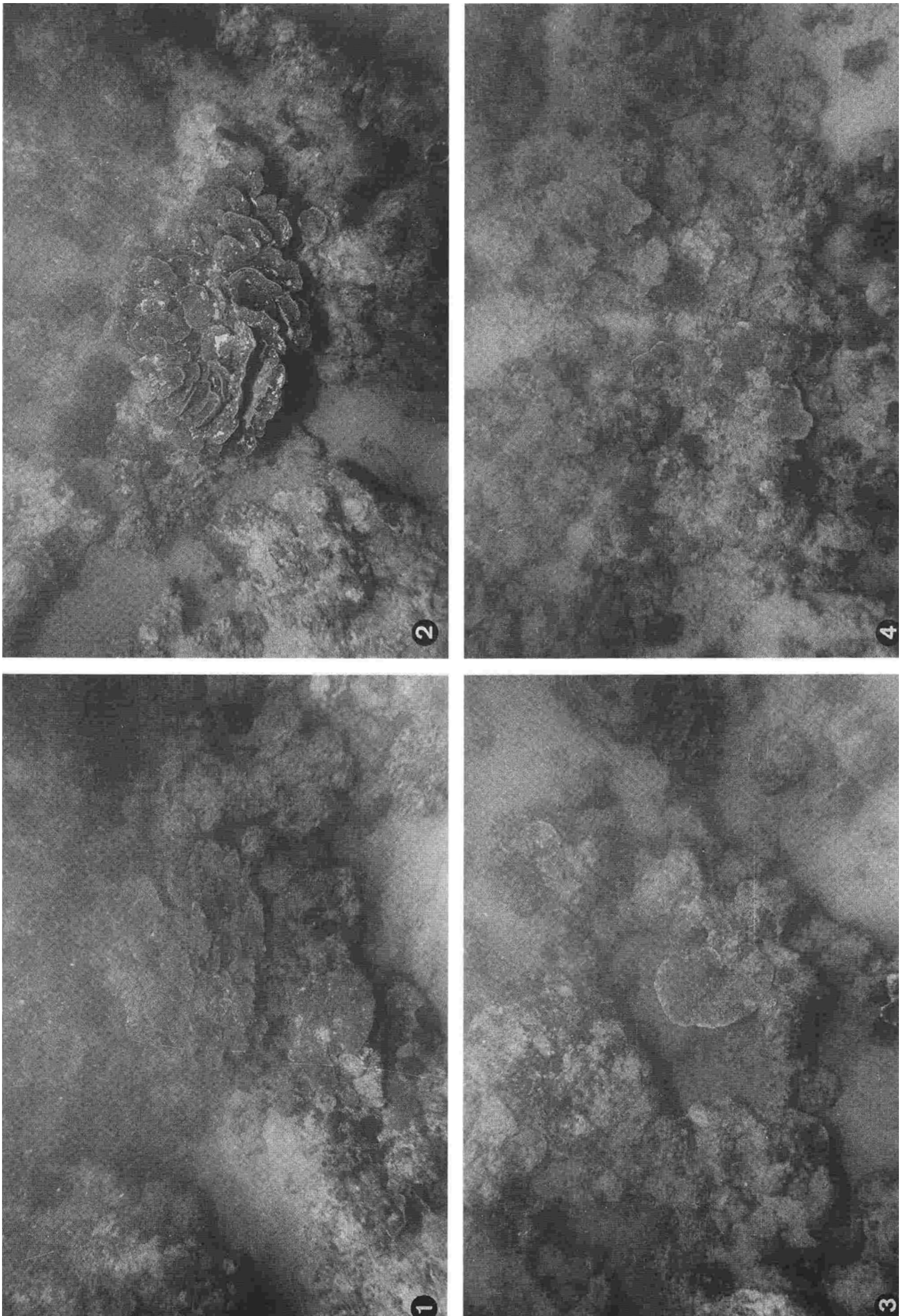
A further modification of the faviid carpet with decreasing light is the platy scleractinian assemblage. Corals become increasingly flat and platy (e.g., *Leptoseris* spp., *Echinophyllia aspera*) to allow maximum light gathering potential. It occurs in the deepest areas, at the lowest limit of coral growth in Safaga Bay. It is best developed on steep slopes and little drop-offs, particularly around the western basin. A high density and diversity of xeniids is also typical in this assemblage.

The occurrence of the *Sarcophyton* carpet is primarily influenced by turbidity (Fig. 3). It is found in areas characterized by slowing longshore currents where sediments and organic material stay in suspension. The high organic load (POM) gives an additional food source to photosynthesis and thus allows the soft corals to outcompete most Scleractinia. Such a mechanism was described by FABRICIUS et al. (1995). The current pattern in the bay suggests that the POM derives largely from the rich seagrass beds and coral carpets upstream of the *Sarcophyton* areas.

The generalized schemes for reefs by ROSEN (1975, 1981) and ours for strong gradient and/or steep relief assemblages (Fig. 3) do not take sedimentation expressly into account. We believe that turbidity and sedimentation are crucial factors in the differentiation particularly of the low gradient and/or low relief assemblages and therefore an additional model had to be developed (Fig. 3). The *Porites* carpet is found in areas of low turbidity and sedimentation. This is supported by the shallower position of the *Porites* carpet relative to the faviid carpet. With increasing turbidity and/or sedimentation the *Porites* carpet grades into a faviid carpet and later a depauperate faviid assemblage. The resilience of faviids against sedimentation is amply demonstrated in the literature (FISHELSON, 1973; RIEGL, 1995 b; RIEGL & BRANCH, 1995; RIEGL & BLOOMER, 1995). Although poritids are capable of withstanding sedimentation (BAK & ELGERSHUIZEN, 1976), we think that they are more adversely affected than Faviidae by the loss of light and thus photosynthetic activity which is concomitant with sedimentation and turbidity (RIEGL & BRANCH, 1995). Therefore, *Porites* is capable of dominating in shallow water areas even when subjected to episodic

Plate 45 The platy scleractinian assemblage in northern Safaga Bay.

Fig. 1. *Pavona yabei* (top centre) and *Oulophyllia crispa* (lower centre) at 30 m depth in the basin of the West area.
Fig. 2. *Turbinaria mesenterina* at 30 m in the basin of the West area.
Fig. 3. *Leptoseris papyracea* (centre) at 30 m depth in the basin of the West area.
Fig. 4. Platy assemblage at 30 m in the basin of the West area with the alcyonacean *Lobophytum* sp. (left), *Sarcophyton glaucum* (centre), various faviids, *Leptoseris papyracea* (centre right), and *Turbinaria mesenterina* (lower centre).



sedimentation pulses during storms (BRAITHWAITE, 1987), but not capable of building a framework in deeper, constantly turbid areas. In such areas individual *Porites* colonies occur frequently, but generally do not form a framework. In the deepest, darkest areas, the faviid carpet is further modified by increasing dominance of platy corals like *Leptoseris* and *Echinophyllia*.

5 CONCLUSION

Clearly defined coral assemblages were found in northern Safaga Bay. They are influenced by hydrodynamics, bottom topography, sedimentation, and turbidity. Two systems under different environmental and ecological control were identified, which also reflect the pronounced topographic differentiation inside the bay. The strong gradient and/or steep relief assemblages (*Acropora* assemblage on windward reefs; *Porites* assemblage on leeward reefs; *Millepora* assemblage on current exposed reefs; *Stylophora* reef flat assemblage) are primarily environmentally controlled due to variable regimes of disturbance frequency by waves, strong currents, and/or drying out during extreme low tides. Most low gradient and/or low relief assemblages, like the coral carpets, experience far lower disturbance frequencies and are primarily biologically controlled.

The described coral assemblages here are characterized by taxa which are easily distinguishable due to their structural typology and/or calyx characteristics. This clear differentiation into assemblages dominated by certain structural types will allow to apply the here presented explanations for community differentiation even in geological situations when taxonomic uniformitarianism is no longer applicable.

ACKNOWLEDGEMENTS

The authors are grateful to A. M. Mansour (South Valley University, Qena) and M. Rasser and M. Zuschin (both Institute of Palaeontology, University of Vienna) for help with field work and fruitful discussions. Photographs were printed by W. Reichmann (Natural History Museum, Vienna) and R. Gold (Institute of Palaeontology, University of Vienna). This study was supported by the "Hochschuljubiläumsstiftung der Stadt Wien", the Austrian Science Foundation (FWF) through project P10715-GEO and an Erwin Schrödinger fellowship to B.R. The paper benefited from constructive comments by W.-Chr. Dullo (Geomar, Kiel) and an anonymous reviewer.

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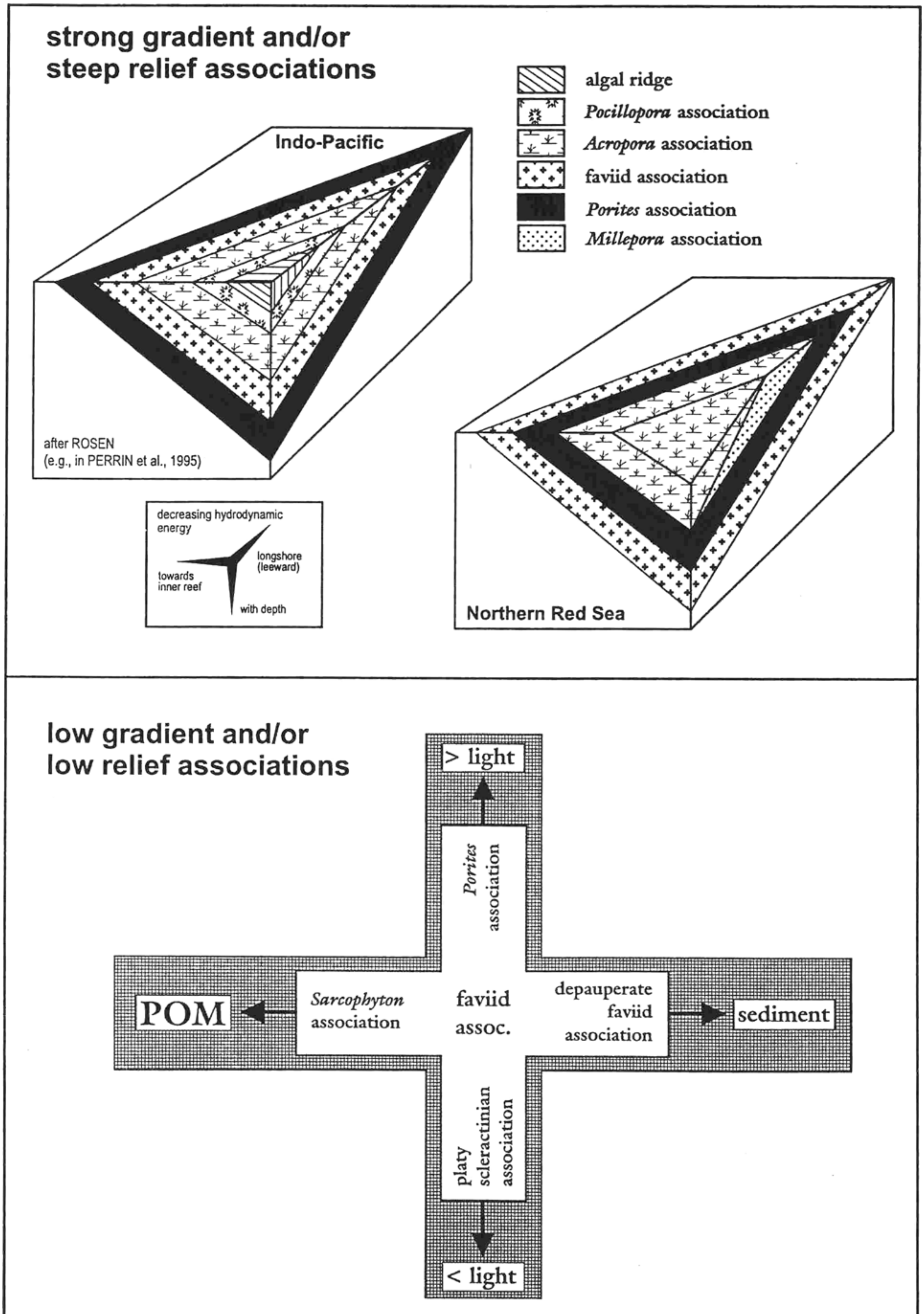

Fig. 3. Schematic relationships of coral assemblages. Upper half: Strong gradient and/or steep relief assemblages. Comparison of Indo-Pacific reefs (after ROSEN (1975, 1981) and PERRIN et al (1995)) and reefs of the northern Red Sea.
Lower half: Low gradient and/or low relief assemblages in the northern Red Sea.

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Manuscript received August 22, 1996

Revised manuscript received November 26, 1996