

## Composition and ecology of deep-water coral associations

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**ABSTRACT:** Between 1966 and 1978 SCUBA investigations were carried out in French Polynesia, the Red Sea, and the Caribbean, at depths down to 70 m. Although there are fewer coral species in the Caribbean, the abundance of Scleractinia in deep-water associations below 20 m almost equals that in the Indian and Pacific Oceans. The assemblages of corals living there are described and defined as deep-water coral associations. They are characterized by large, flattened growth forms. Only 6 to 7 % of the species occur exclusively below 20 m. More than 90 % of the corals recorded in deep waters also live in shallow regions. Depth-related illumination is not responsible for depth differentiations of coral associations, but very likely, a complex of mechanical factors, such as hydrodynamic conditions, substrate conditions, sedimentation etc. However, light intensity determines the general distribution of hermatypic Scleractinia in their bathymetric range as well as the platelike shape of coral colonies characteristic for deep water associations. Depending on mechanical factors, *Leptoseris*, *Montipora*, *Porites* and *Pachyseris* dominate as characteristic genera in the Central Pacific Ocean, *Podabacia*, *Leptoseris*, *Pachyseris* and *Coscinarea* in the Red Sea, *Agaricia* and *Leptoseris* in the tropical western Atlantic Ocean.

### INTRODUCTION

Considerable attention has been paid to shallow-water coral associations since the first half of this century (Duerden, 1902; Mayer, 1918; Umbgrove, 1939). Detailed investigations at depths down to 20 m became possible only through the use of autonomous diving apparatus. SCUBA diving encounters limitations at greater depths due to technical, physiological and methodological problems, and only few studies have been conducted at depths exceeding 30 m (Roos, 1964; Pichon, 1972, 1977; Goreau & Goreau, 1973; Goreau & Land, 1974; Kühlmann, 1974a; Bak, 1977; Sheppard, 1980, 1981). SCUBA techniques provide the most detailed and precise method for investigating composition and ecology of deep-water coral associations.

### METHODS

Steep slopes with relatively monotonous surfaces of coral reefs were chosen as study sites in order to avoid complications due to bottom unevenness. The investigations were carried out between the water surface and 70 m depth, employing standard SCUBA techniques.

Hermatypic corals were collected in order to facilitate taxonomic determination.

Data on depth occurrence, listed in tables without references, were extracted from publications by Klunzinger (1879), Quelch (1886), Gardiner (1898, 1904, 1905), Vaughan (1907, 1918), Mayer (1918), Horst (1922), Matthai (1924), Hoffmeister (1925), Thiel (1932), Umbgrove (1940), Crossland (1952), Wells (1954, 1971, 1973), Goreau & Wells (1967), Chevalier (1971, 1975), Wijsman-Best (1972, 1977), Yamazato (1972), Goreau & Goreau (1973), Scheer & Pillai (1974), Pillai & Scheer (1976), Veron & Pichon (1976, 1979), Scatterday (1977), Veron, Pichon & Wijsman-Best (1977), Faure & Pichon (1978), Rosen (1978), Wallace (1978), Dinesen (1980), Zlatarski & Estalella (1982). Uncertain data regarding maximum depths (obtained by dredging) are represented in the form of dotted lines. Only definite values based on own visual observations have been expressed as straight lines. Values taken from literature are expressed by dashes in Tables 4 and 5. Data on depth occurrence reported in the literature could be complemented in 71 cases.

#### DEEP-WATER CORAL ASSOCIATIONS

My results are presented here from East to West, i.e. in the order Pacific Ocean, Red Sea, western Atlantic Ocean.

Takapoto is a flat atoll covered by coconut palms. It belongs to the Tuamotu Archipelago situated 145°10' W and 14°40' S. Its outer slopes fall sharply to a depth of more than 2500 m. Its lagoon measures 6 × 20 km, and is more than 30 m deep. The lagoon contains some patch reefs, either isolated or arranged in groups. Takapoto is a purely oceanic coral atoll, affected neither by terrigenous nor by local anthropogenic



Fig. 1. On the leeward slope, in calm waters (25–30 m deep), *Synarea convexa* with its large, flattened, deep-water shape is predominant. Takapoto Atoll, Tuamotus. (Photo: D. H. H. Kühlmann)

substances. I have studied both the windward and leeward sides of the outer atoll slopes and patch reefs in the lagoon. At first, the windward side slopes gradually from the shore seawards, then, at a depth of 20 to 25 m, steeply at an angle of 60°. The leeward slope starts to fall at an angle of 50 to 90° from 12 to 15 m. Both slopes are characterized by good and comparable light and visibility conditions: at a depth of 20 m, visibility is 40 m; at 40 m, 20 m; at 50 m, 12 m; at 70 m, 5 m (Kühlmann, 1970b). However, the plate-shaped colonies of *Synaraea* and *Leptoseris* dominate on the leeward slope (Fig. 1), while the windward slope is dominated by *Porites* and *Montipora* colonies which are flattened like shingles (Fig. 2). This remarkable difference will be discussed later.

The water in the lagoon differs from that in the open ocean: it has a higher salinity, due to higher evaporation (Caspers, 1968, 1981; Hauti, pers. comm.); it is wind-protected and therefore less intermixed; it contains heavy suspensions and is more turbid. Hence, except the 3 euryoecious species *Acropora* cf. *valida*, *Pavona varians* and *Porites australiensis*, all others occur either on the outer slopes or in the lagoon. There are also differences in the composition of the coral associations on the outer slopes: 16 species were found in both habitats; 7 species were found exclusively on the windward slope, and 10 exclusively on the leeward slope. Table 1 lists the composition of the Takapoto deep-water coral associations of the outer slopes leeward (Fig. 1) and windward (Fig. 2) and of the patch reefs in the lagoon.

M o o r e a lies in the vicinity of Tahiti. It is one of the Society Islands and is located

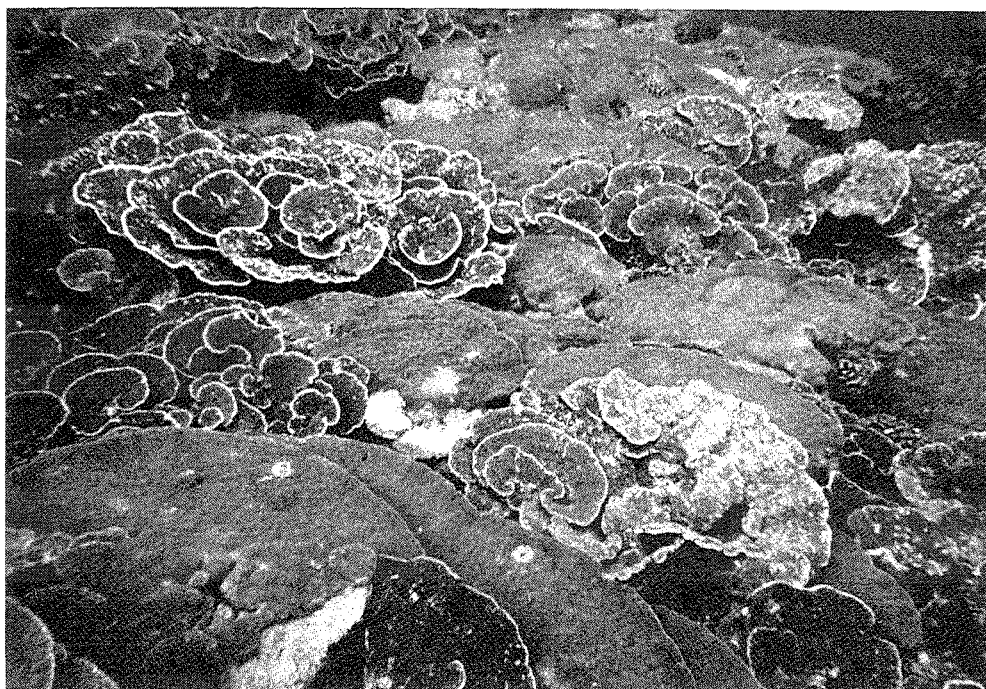


Fig. 2. On the windward slope with its strong water movement a deep-water coral association grows at a depth of 25 m with flattened *Porites australiensis*, *Montipora verrilli* and some branched *Pocillopora verrucosa*. Takapoto Atoll, Tuamotus. (Photo: D. H. H. Kühlmann)

149°50' W and 17°30' S. Of volcanic origin, it consists of a large crater whose northern part has collapsed and sunk beneath the water surface (Chevalier, 1973). Although it measures only about 23 × 30 km, the peak of its jagged crater crown is as high as 1212 m. The ocean around the island is more than 1500 m deep. The island is encircled by a barrier reef, the sides of which slope down more or less steeply to 30 to 40 m, abutting on a bottom covered with sand and debris. The steep slope continues to depths

Table 1. Deep-water coral associations of the Takapoto Atoll, Tuamotus, Pacific; + = 20 to 40 m deep; > = deeper than 40 to 70 m

Species	Outer slope		Lagoon
	Windward	Leeward	
<i>Porites australiensis</i> Vaughan, 1918	+	+>	+
<i>Leptastrea transversa</i> Klunzinger, 1879	+	+>	+
<i>Acropora</i> cf. <i>valida</i> (Dana, 1846)	+	+	+
<i>Astreopora myriophthalma</i> (Lamarck, 1816)	+	+>	
<i>Pavona varians</i> Verrill, 1864	+	+>	
<i>Fungia concinna</i> Verrill, 1864	+	+>	
<i>Millepora platyphylla</i> Ehrenberg, 1834	+	+	
<i>Pocillopora elegans</i> Dana, 1846	+	+	
<i>Pocillopora verrucosa</i> (Ellis et Solander, 1786)	+	+	
<i>Montipora verrilli</i> Vaughan, 1907	+	+	
<i>Leptoseris incrustans</i> (Quelch, 1886)	+	+	
<i>Pavona clavus</i> (Dana, 1846)	+	+	
<i>Herpolitha limax</i> (Esper, 1797)	+	+	
<i>Porites lutea</i> Edwards et Haime, 1851	+	+	
<i>Favia stelligera</i> (Dana, 1846)	+	+	
<i>Acanthastrea echinata</i> (Dana, 1846)	+	+	
<i>Leptoseris mycetoseroides</i> Wells, 1954	+		
<i>Pachyseris speciosa</i> (Dana, 1846)	+		
<i>Porites lichen</i> Dana, 1846	+		
<i>Echinopora</i> cf. <i>lamellosa</i> (Esper, 1795)	+		
<i>Echinophyllia aspera</i> (Ellis et Solander, 1786)	+		
<i>Leptoseris porosa</i> (Quelch, 1886)	>		
<i>Fungia</i> cf. <i>granulosa</i> Klunzinger, 1879	>		
<i>Pocillopora</i> cf. <i>solida</i> Quelch, 1886		+>	
<i>Synaraea convexa</i> Verrill, 1864		+>	
<i>Acropora danai</i> (Edwards et Haime, 1860)		+	
<i>Acropora nasuta</i> (Dana, 1846)		+	
<i>Acropora rambleri</i> (Basset-Smith, 1890)		+	
<i>Montipora</i> cf. <i>tuberculosa</i> (Lamarck, 1816)		+	
<i>Gardineroseris planulata</i> (Dana, 1846)		+	
<i>Leptoseris fragilis</i> Edwards et Haime, 1849		+	
<i>Pavona maldivensis</i> (Gardiner, 1905)		+	
<i>Fungia paumotensis</i> Stutchbury, 1833		+	
<i>Stylocoeniella guentheri</i> Basset-Smith, 1890			+
<i>Psammocora</i> cf. <i>contigua</i> (Esper, 1797)			+
<i>Montipora verrucosa</i> (Lamarck, 1816)			+
<i>Favia speciosa</i> (Dana, 1846)			+
<i>Leptastrea purpurea</i> (Dana, 1846)			+
<i>Platygyra daedalea</i> (Ellis et Solander, 1786)			+
<i>Lobophyllia corymbosa</i> (Forsk. 1775)			+

of more than 60 m where passages in front of river mouths cause a break in the barrier reef. The steep slopes of the patch reefs in the lagoon reach depths of 20 to 30 m. In the northeastern corner of the island, the barrier reef has become a fringing reef (Chevalier, 1977). Coral associations of the seaward slope have grown along the northern barrier reef which, in its central part, is relatively well protected from the wind, although it is exposed to strong-to-moderate currents. Currents are stronger in the northwestern and, in particular, northeastern waters. The slopes incline, in many different ways, towards the sea at angles of 5 to 35° forming reef tongues. Dominant shrubby growth forms extend far down. Typical flattened deep-water coral associations become – at first gradually then increasingly – intermingled with shallow-water forms at 30 m. Terrigenous suspensions from rivers and brooks as well as increasing depths reduce light and visibility: it is 20 m at 20 m depth; 10 m at 40 m, and 5 m at 50 m. Corals at a depth of 40 to 50 m stem from rubble plains of the sandy zone in front of the reef which have a seaward inclination of 7 to 10°. Of the 35 species occurring on the outer slope of the barrier reef at a depth of 30 or 40 m, 15 species also live in the rubble zone of the fore reef.

The lagoon behind the barrier reef is influenced by the sea entering it by several channels. This is perhaps the reason why 28 of a total of 43 species live both on the outer slope and in the lagoon. The 3 species found only on the patch reefs of the lagoon of Moorea are *Psammocora explanulata*, *P. nierstraszi* and *P. cf. obtusangula*. Considering the presence of *P. cf. contigua* in the lagoon of Takapoto, the genus *Psammocora* seems to be particularly adapted to this habitat; if so, *P. profundacella*, which I found only on the outer slope of Moorea, is a biological exception to this rule. Table 2 lists the diversity of the deep-water coral associations below 20 m in the open sea and in the lagoon of Moorea.

W i n g a t e R e e f, 37°18' E and 19°38' N, is situated 3 nautical miles northeast of Port Sudan in the Red Sea and extends about 8 km in a northeasterly direction. It follows the contours of the coast, north of Port Sudan. It is a barrier reef which has grown on a mountain crest. Forming several terraces, its outer slope inclines seawards to depths of more than 700 m, and landwards down to 413 m. Its eastbound outer slope at first falls to a depth of 18 to 22 m in an irregular fashion, then continues falling steeply as a vertical or slightly overhanging rock wall. An overhanging ledge at its bottom is covered with Gorgonacea hanging downwards. At 30 to 35 m a slope with an inclination of 60° extends into a depth of 70 to 80 m, and then again falls vertically. A slight current flows from north to south in accordance with the main wind direction. The water is clear and well illuminated due to an almost constantly cloudless sky.

While the perpendicular wall is only sparsely covered with corals, the steep slope underneath at first displays a much denser abundance, followed abruptly by an area nearly clear of corals from 50 m onward. While the sparse colonization of the rock wall is due to the vertical or slightly, overhanging substrate, unsuitable for coral growth, the abrupt reduction in abundance below 50 m is possibly due to a general reduction of light intensity to below the minimum necessary, accompanied by a thermocline at that depth and a drop in water temperature from 31 to 28 °C in August. With 52 species occurring below 20 m, the diversity of species is fairly high (Table 3). One of the two *Stylophora* species, *St. mamillata*, occurs at depths between 20 and 40 m; the other, *St. kuehlmanni*, between 20 and 70 m. Both are typical components of local deep-water coral associa-

tions. However, in general, the foliaceous or disk-shaped forms of *Leptoseris*, *Coscinarea*, *Mycedium*, *Pachyseris*, *Pavona*, *Podabacia*, *Echinopora*, *Echinophyllia* and the crustose colonies of *Psammocora*, *Montipora*, *Porites*, *Favia*, *Favites* and *Leptastrea* were dominant.

Table 2. Deep-water coral associations of Moorea, Society Islands, Pacific

Species	Outer slope 20–35 m	Fore reef 35–45 m	Lagoon 20–36 m
<i>Stylocoeniella guentheri</i> Bassett-Smith, 1890	+	+	+
<i>Acropora granulosa</i> (Edwards et Haime, 1860)	+	+	+
<i>Astreopora myriophthalma</i> (Lamarck, 1816)	+	+	+
<i>Montipora composita</i> Crossland, 1952	+	+	+
<i>Pavona varians</i> Verrill, 1864	+	+	+
<i>Leptastrea purpurea</i> (Dana, 1846)	+	+	+
<i>Montastrea curta</i> (Dana, 1846)	+	+	+
<i>Acanthastrea echinata</i> (Dana, 1846)	+	+	+
<i>Psammocora profundacella</i> Gardiner, 1898	+	+	
<i>Pocillopora</i> cf. <i>solida</i> Quelch, 1886	+	+	
<i>Pocillopora verrucosa</i> (Ellis et Solander, 1786)	+	+	
<i>Acropora</i> cf. <i>valida</i> (Dana, 1846)	+	+	
<i>Montipora verrucosa</i> (Lamarck, 1816)	+	+	
<i>Porites australiensis</i> (Vaughan, 1918)	+	+	
<i>Cyphastrea serailia</i> (Forsk. 1775)	+	+	
<i>Montipora</i> cf. <i>minuta</i> Bernard, 1897	+		+
<i>Montipora</i> cf. <i>tuberculosa</i> (Lamarck, 1816)	+		+
<i>Leptoseris incrustans</i> (Quelch, 1886)	+		+
<i>Leptoseris mycetoseroides</i> Wells, 1954	+		+
<i>Pachyseris speciosa</i> (Dana, 1846)	+		+
<i>Pavona maldivensis</i> (Gardiner, 1905)	+		+
<i>Fungia concinna</i> Verrill, 1864	+		+
<i>Fungia repanda</i> Dana, 1846	+		+
<i>Herpolitha limax</i> (Esper, 1797)	+		+
<i>Porites lutea</i> Edwards et Haime, 1851	+		+
<i>Synaraea convexa</i> Verrill, 1864	+		+
<i>Leptastrea transversa</i> Klunzinger, 1879	+		+
<i>Acropora exilis</i> (Brook, 1893)	+		
<i>Acropora</i> cf. <i>variabilis</i> (Klunzinger, 1879)	+		
<i>Montipora verrilli</i> Vaughan, 1907	+		
<i>Gardineroseris planulata</i> (Dana, 1846)	+		
<i>Napopora irregularis</i> Quelch, 1886	+		
<i>Synaraea irregularis</i> Verrill, 1864	+		
<i>Favia stelligera</i> (Dana, 1846)	+		
<i>Lobophyllia costata</i> (Dana, 1846)	+		
<i>Psammocora explanulata</i> Horst, 1922			+
<i>Psammocora nierstraszi</i> Horst, 1921			+
<i>Psammocora</i> cf. <i>obtusangula</i> (Lamarck, 1816)			+
<i>Montipora erythraea</i> Marenzeller, 1906			+
<i>Montipora</i> cf. <i>floweri</i> Wells, 1954			+
<i>Montipora spumosa</i> (Lamarck, 1816)			+
<i>Fungia paumotensis</i> Stutchbury, 1933			+
<i>Echinophyllia aspera</i> (Ellis et Solander, 1786)			+

Table 3. Deep-water coral association of the Wingate Reef off Port Sudan, Red Sea

Species	Outer steep slope			
	20–30 m	30–40 m	40–50 m	50–70 m
<i>Stylophora kuehlmanni</i> Pillai et Scheer, 1982	+	+	+	+
<i>Leptoseris explanata</i> Yabe et Sugiyama, 1941	+	+	+	+
<i>Leptoseris mycetoseroides</i> Wells, 1954	+	+	+	+
<i>Coscinarea monile</i> (Forsk., 1775)	+	+	+	+
<i>Alveopora verrilliana</i> Dana, 1872	+	+	+	+
<i>Mycedium elephantotus</i> (Pallas, 1766)	+	+	+	+
<i>Psammocora profundacella</i> Gardiner, 1898	+	+	+	
<i>Acropora granulosa</i> (Edwards et Haime, 1860)	+	+	+	
<i>Montipora meandrina</i> (Ehrenberg, 1834)	+	+	+	
<i>Montipora stilosa</i> (Ehrenberg, 1834)	+	+	+	
<i>Pachyseris speciosa</i> (Dana, 1846)	+	+	+	
<i>Pavona yabei</i> Pillai et Scheer, 1976	+	+	+	
<i>Fungia fungites</i> (Linné, 1758)	+	+	+	
<i>Podabacia crustacea</i> (Pallas, 1766)	+	+	+	
<i>Porites echinulata</i> Klunzinger, 1879	+	+	+	
<i>Porites lutea</i> (Edwards et Haime, 1851)	+	+	+	
<i>Synaraea undulata</i> Klunzinger, 1879	+	+	+	
<i>Echinopora gemmacea</i> (Lamarck, 1816)	+	+	+	
<i>Echinopora lamellosa</i> (Esper, 1795)	+	+	+	
<i>Favia pallida</i> (Dana, 1846)	+	+	+	
<i>Favites abdita</i> (Ellis et Solander, 1786)	+	+	+	
<i>Favites complanata</i> (Ehrenberg, 1834)	+	+	+	
<i>Stylophora danae</i> Edwards et Haime, 1850	+	+		
<i>Stylophora mamillata</i> Pillai et Scheer, 1982	+	+		
<i>Gardineroseris planulata</i> (Dana, 1846)	+	+		
<i>Leptoseris fragilis</i> Edwards et Haime, 1849	+	+		
<i>Pavona varians</i> Verrill, 1864	+	+		
<i>Fungia repanda</i> Dana, 1846	+	+		
<i>Goniastrea pectinata</i> (Ehrenberg, 1834)	+	+		
<i>Galaxea cf. astreata</i> (Lamarck, 1816)	+	+		
<i>Lobophyllia hemprichi</i> (Ehrenberg, 1834)	+	+		
<i>Dendrophyllia arbuscula</i> Horst, 1922	+	+		
<i>Stylocoeniella guentheri</i> Bassett-Smith, 1890	+			
<i>Psammocora explanulata</i> Horst, 1922	+			
<i>Pocillopora damicornis</i> (Linné, 1758)	+			
<i>Seriatopora hystrix</i> Dana, 1846	+			
<i>Leptoseris scabra</i> Vaughan, 1907	+			
<i>Pavona cactus</i> (Forsk., 1775)	+			
<i>Pavona maldivensis</i> (Gardiner, 1905)	+			
<i>Goniopora tenella</i> (Quelch, 1886)	+			
<i>Galaxea fascicularis</i> (Linné, 1767)	+			
<i>Echinophyllia aspera</i> (Ellis et Solander, 1786)	+			
<i>Psammocora haimeana</i> Edwards et Haime, 1851		+	+	
<i>Cyphastrea micropthalma</i> (Lamarck, 1816)		+	+	
<i>Favia speciosa</i> (Dana, 1846)		+	+	
<i>Porites solida</i> (Forsk., 1775)			+	
<i>Favites pentagona</i> (Esper, 1794)			+	
<i>Astreopora myriophthalma</i> (Lamarck, 1816)		+		
<i>Favites peresi</i> Faure et Pichon, 1978		+		
<i>Leptastrea purpurea</i> (Dana, 1846)		+		
<i>Platygyra daedalea</i> (Ellis et Solander, 1786)		+		
<i>Plerogyra sinuosa</i> (Dana, 1846)		+		

St. Croix, one of the Virgin Islands, is situated 64°50' W and 17°45' N. The island extends over an area of about 15 × 30 km. Lying southeast of Puerto Rico, the island belongs geologically to the Greater Antilles, geographically to the Lesser Antilles. There are several reefs near the coast. The north-western coast of St. Croix first slopes down to a depth of 10 m at an angle of 5 to 10°; then at 30 to 40° to 20 m, and at 70 to 80° to 50 m. Below that, covered with sponges and Antipatharia, the sea bottom slopes vertically to depths of more than 1000 m. The water is clear with few suspensions. The influence of the Atlantic swell is considerable, and a slight current flows westwards along the coast. The deep-water coral association covers the steep slope between 25 and 50 m with an abundance of 80 %. It consists of the following 13 species: *Stephanocoenia michelini*, *Agaricia agaricites*, *A. fragilis*, *A. grahamae*, *A. lamarcki*, *A. undata*, *Siderastrea siderea*, *Montastrea annularis*, *M. cavernosa*, *Mycetophyllia alicae*, *M. danaana*, *Scolymia lacera*, *Eusmilia fastigiata*. The slope is densely covered with flattened corals, particularly *A. lamarcki* and the disk-shaped ecomorphous *A. agaricites* f. *purpurea* as well as a number of other *Agaricia* species (Table 5). Their forms resemble shingles or plates. *Montastrea annularis* and *M. cavernosa* are mainly crusty, although at 30 m and below they form thick projecting lips and shingles. *Eusmilia fastigiata* grows in recesses.

Cuba, the largest island of the Antilles, is surrounded by many coral reefs and island chains (Kühlmann, 1970a, 1974b). Adjacent to several seas, the sublittoral region is exposed to various hydrographic and atmospheric influences, such as different currents, winds and river mouths (Kühlmann, 1970b). Steep walls falling to a depth of more than 300 m occur sporadically near the shoreline of certain bays. Similar to the St. Croix investigation area, there is, on the west side of the Bay of Matanzas at 80°40' W and 23° N, a fringing reef gradually sloping down from the shore and leading to a steep slope at a depth of 6 m which, interspersed by a few narrow steps, continues at an angle of 60 to 80° into the depths (Kühlmann, 1974a). The water is clear, even though the hydrodynamics of this protected location cause a slight and continuous sedimentation, as shown by fine silt layers covering the irregular surface of the steep slope. 60 % of the latter was covered by the following 13 Scleractinia: *Stephanocoenia michelini*, *Madracis formosa*, *Agaricia agaricites*, *A. fragilis*, *Leptoseris cucullata*, *Siderastrea siderea*, *Porites astreoides*, *Colpophyllia natans*, *Montastrea cavernosa*, *Meandrina meandrites*, *Mycetophyllia lamarckiana*, *Scolymia cubensis*, *Eusmilia fastigiata* and the hydrocoral *Stylaster roseus*. Below 12 m the crustaceous shingle- and disk-type forms are so dominant that the slope looks like a deep-water coral association.

## DISCUSSION

Most of the corals belonging to the deep-water associations occur also in shallow waters at depths less than 5 m. The general bathymetric range of the Indopacific species considered here is listed in Table 4; for Caribbean species consult Table 5 as well as the publications of Goreau & Wells (1967) and Wells (1973). All in all, species of hermatypic corals grow in so broad a depth belt that changes in light intensity and quality, associated with the selective absorption by the waters (Scheer, 1966; Jerlov, 1968, 1970; Kühlmann, 1970b; Jaubert & Vasseur, 1974), cannot be regarded as the reason for a differentiated depth distribution of most Scleractinia species, as pointed out elsewhere



(Loya, 1972; Kühlmann, 1980; Dinesen, 1982; Sheppard, 1982). Scatterday (1977) noted that "Many species seem, on the basis of observations made in only one or a few localities, to be in different depths elsewhere".

Dustan (1979) demonstrated for *Montastrea annularis* that zooxanthellae (*Gymnodinium microadriaticum*) are in a position to photo-synthesize in a wide range of light intensities and spectral ranges. His findings based on investigations carried out by Goreau & Wells (1967), explain why individual colonies of this coral species are able to live in depths ranging from 0 to 95 m. Therefore, symbiotic algae of hermatypic corals seem to be adapted to a wide range of light intensities; their optimum, however, is in subdued underwater light. Falkowsky & Dubinski (1981), investigating transplanted *Stylophora pistillata*, discovered that shade-adapted individuals are able to adapt to well illuminated habitats after 4 to 8 weeks, perhaps by means of light-dependent changes in the size of the chloroplasts. Wetthey & Porter (1976) suggest, on the basis of experiments with some species of reefbuilding corals, "that given a particular light regime, the algal photosynthetic efficiency, relative to the maximum photosynthetic rate, is independent of the coral species which the algae inhabit". Experiments with ammonia demonstrate that increase of calcification is associated with an elevated rate of photosynthesis (Taylor, 1978). But subsaturation and variation of light are compensated by both endosymbiotic algae and hermatypic corals; presumably the investigated Scleractinia are mainly independent of the particular environmental light conditions (Beyers, 1966; Barnes & Taylor, 1973; Roth, 1975; Chalker & Taylor, 1978). For both *Acropora cervicornis* and *Gymnodinium microadriaticum* maxima of calcification and photosynthetic capacity occurred at sunrise and sunset, but diminished in constant bright illumination (Chalker, 1977). Ditlev (1978) pointed out that the zooxanthellae of *Coeloseris mayeri* migrate into deeper tissue layers if exposed to high light intensities. Fricke & Vareschi (1982) observed special organs in *Pleurogyra sinuosa* full of zooxanthellae, which can be erected or contracted according to the light conditions of the environment. Lasker (1977, 1981) suggests the existence of two morphs in *Montastrea cavernosa*: a diurnal one (with greater zooxanthellae densities) and a nocturnal one – perhaps another way of adaptation to different light qualities and quantities. Stiévenart (1975) also pointed out that there are two different ecological populations, one at a depth of 9 m, the other at a depth of 30 m. Not all processes of light adaptations by hermatypic corals and, in particular, by their zooxanthellae are clear, and some of the relevant investigations came to conflicting conclusions (Chalker & Taylor, 1975).

According to Stiévenart (1975a, b) average amounts of symbiotic algae and the ratio of chlorophyll c / chlorophyll a in *Mycetophyllia lamarckiana* decrease as depth increases. In contrast, Zvalinsky et al. (1978) found in "Acropora" from shallow waters, caves and from depths of 30–40 m that, parallel with decreasing light intensities, the number of zooxanthellae and simultaneously the content of photosynthetic pigments increase.

All results presented here lead to the assertion that hermatypic coral species are generally light-dependent because of their symbiosis with zooxanthellae, but most of them can compensate in a different manner for the daily and local variations in the quantity of light, even at greater depths, although metabolism and growth rates vary according to the degree of deviation from the optimum (Strömberg, 1976; Barnes & Crossland, 1978). Consequently, differing degrees of turbidity reduce or extend the









average depth distributional belt of hermatypic corals as a whole, but do not influence the depth occurrence of the individual coral species.

This is corroborated by the occurrence of the Agariciidae deep-water association below 12 m at Matanzas, while it occurs below 25 m off St. Croix. The water is clear and well illuminated in both habitats, but the site of the Bay of Matanzas is very much more protected (Kühlmann, 1974a); thus, water movement is just as reduced here at a depth of 12 m as off St. Croix at 25 m. Nor can light be held responsible for the varying bathymetric occurrence of Caribbean deep-water coral associations; it is more likely that different hydrodynamic conditions and other controlling factors exert the decisive influence (Kühlmann, 1971).

Individual species have the same pattern of behaviour: *Napopora irregularis* is not rare at a depth of 10 m on the outer slopes of Moorea, while in particularly clear and agitated waters it is dominant at depths between 25 and 35 m. Yet this species is also found in shallow lagoons at a depth of 1 m, if clear water is continuously driven over the reef edge and strongly agitated by the tradewind. The example shows clearly that the species is independent of a certain light quality and quantity. It is important to keep in mind that there is an equal occurrence of most coral species in deep and shallow waters (Tables 4, 5), if hydrodynamical conditions, substrate and sedimentation are comparable (Kühlmann, 1977, 1980).

The situation is somewhat different as regards the Takapoto deepwater coral associations, which differ greatly in terms of species composition. The outer slope on the windward side is dominated by large *Porites australiensis* and *Synaraea convexa* and *Leptoseris incrustans*, while *Platygyra daedalea* and *Lobophyllia corymbosa* are predominant on the steep slopes situated in the depths of the lagoon. Although the latter occur under the influence of a stronger sedimentation in more turbid water and the effects of lack of light cannot therefore be excluded, the outer slopes on the windward and leeward sides still have the same clear water with optimum light conditions. Accordingly, this is another case where light is not a factor affecting the depth of coral species. The deep-water coral associations, nonetheless typified by varying dominant species, are dependent on the hydrodynamic conditions which differ greatly in the two habitats. The windward shore is under the strong influence of the tradewind, but the leeward shore is sheltered.

Hence the term "deep-water corals" must not be associated with the light factor, and changes in light intensity do not result necessarily in changes of species composition, as has been suggested in the past (Jaubert & Vasseur, 1973; Mergner & Scheer, 1974), because most species live in both shallow and deep waters. On the noxious effects of UV radiation Siebeck (1981) concluded: "Considering the highly vertical UV gradients due to the exponential drop in radiation, it is obvious that ultraviolet light is important not only for the presence or absence of the various species of organisms, but also for their vertical distribution within the upper reef region, in that portion influenced by UV light." Simultaneously, he observed *Turbinaria mesenterina* colonies at a depth of 5–6 m to be more sensitive to UV radiation than those occurring at a depth of 1–2 m. Jokiel & York (1982) found that *Pocillopora damicornis* treated with UV-light during the growth phase contained a greater concentration of the "S-320" UV-absorbing substances than corals living in filtered sunlight, lacking solar ultraviolet. This species is capable of adapting to various intensities of UV light and of existing in different depths. Mucus is

secreted plentifully by the stony corals if they are in extremely shallow water or when taken out of the water for examination. This mechanism, besides being a safeguard against desiccation, is also a safeguard against UV damage. It is possible that the symbiotic zooxanthellae also operate as a protective factor against UV radiation, since hermatypic corals generally grow on fully exposed, insolated substratum without any damage. On the other hand, hermatypic but aposymbiotic corals, such as *Dendrophyllia arbuscula*, *Tubastrea* cf. *coccinea* and *Phyllangia pallida* in the Red Sea and *Tubastrea coccinea*, *Astrangia solitaria* and *Phyllangia americana* in the Caribbean region settle only in dark shady places of the reefs because of lacking symbiotic algae. Thus, UV radiation is not responsible for the vertical distribution of several hermatypic symbiotic scleractinians. The term "deep-water coral" should be determined more precisely, whereby the findings made so far relate solely to the status of the species considered and not to the ecological growth forms of hermatypic corals.

Flattened growth – considered to be typical of many of the coral colonies growing in deep water (Kawaguti, 1937; Goreau, 1963; Barnes, 1973; Faure, 1974; Bonem & Stanley, 1977; Meischner & Meischner, 1977) – is perhaps light-dependent, unlike depth occurrence of the species involved. This is particularly evident in stony coral species which form massive colonies in shallow or medium-deep waters, becoming increasingly flatter in deeper waters. Goreau (1959) and Dustan (1979) ascribed this phenomenon to a reduction in the output of calcium carbonate because of a lower photosynthetic rate. Since the spherical form has the largest volume with a small surface, the flattened form can be considered an expression of the economy of skeleton material. That is why coral species occurring as massive colonies in shallow waters, such as *Porites lutea*, *Montastrea annularis*, *Echinopora lamellosa*, *Favia speciosa* and others, form flattened lips and overlapping shingles at greater depths. On the other hand, the soft leaf and disk-shaped colonies, which offer the water large surfaces to act on, would be immediately destroyed in shallow or medium-deep water. *Favia stelligera* colonies, which are column-shaped in shallow waters, are flat at greater depths. Shrublike forms such as *Acropora granulosa*, *A. danai* and *A. rambleri* are characterized by flattened branches in deeper waters. The most numerous species in deep-water regions are those which grow solely or predominantly in the shape of a disk: they include *Leptoseris incrustans*, *L. mycetoseroides*, *Pachyseris speciosa*, *Podabacia crustacea*, *Coscinarea monile* and others.

Even the orientation on the substrate of these coral colonies is characteristic. Crustacean colonies such as some *Montipora* and *Psammocora* species and *Stylophora mamillata* follow the relief of the substrate. Even large, disk-shaped corals such as *Agaricia*, *Leptoseris*, *Podabacia* and *Pachyseris* are orientated vertically. Small disk or leaf-shaped colonies such as *Agaricia lamarcki* and *Synaraea* species may also be horizontally oriented. Scleractinia, such as *Favia*, *Favites*, *Montastrea* and *Porites* species, which are flattened in deep water while otherwise being massive, have a horizontal or, particularly the large colonies, a downwards-inclined active surface. Branching species, such as *Acropora*, *Madracis* and *Stylophora kuehlmanni*, also grow horizontally. Only *St. kuehlmanni* displays branches directed upwards even in deep-water regions, provided that it grows on a horizontal rocky bottom.

As a result of investigations on flat slopes in the medium-depth range, Loya (1972) pointed out that, as a rule, the size of the colonies decreases as depth increases.

However, in the deep-water range of the steep slopes investigated, between 20 and 40 m, large colonies predominate. The disks, plates and lips formed by *Agaricia agaricites* f. *purpurea*, *Leptoseris cucullata*, *Porites australiensis* and *Leptoseris incrustans* often have a diameter exceeding 1 m, while the diameter of *Agaricia undata*, *Podabacia crustacea*, *Pachyseris speciosa* and *Leptoseris mycetoseroides* may be more than 0,5 m. Such gigantism of the colonies must probably be attributed to the greatly subdued hydrodynamic conditions. While coral colonies in shallow waters are broken down relatively frequently by high, rough waves, as demonstrated by the huge dams and dunes of debris on the shores (Kühlmann, 1970a, 1980), coral colonies in deep-water zones are usually not subjected to violent water movement. While corals in shallow waters have to resettle again and again and, apart from particularly robust Poritidae, Faviidae and some others, are able to form only small or medium-sized colonies resulting from the destructive action of storms, the deep-water-zone corals have plenty of time to form large and broad colonies even at slow growth rates. In short, deep-water coral associations existing between depths of 20 and 50 m are mainly flattened, large, obliquely or vertically orientated growth forms of hermatypic symbiotic Scleractinia. The frequent deep-water growth forms are, together with the few species growing solely in deep water, designated by the ecological term "deep-water corals" which should in no way be confused with the ahermatypic "deep-sea corals" living in the aphotic zone.

Below 40 to 50 m, a decrease in size of the colonies is accompanied by a distinct decrease of coral growth. It can be concluded that the optimum deep-water zone is between 20 and 50 m, provided there are favourable turbidity and light conditions. As has been shown by the example of the Takapoto Atoll, a differentiation of coral

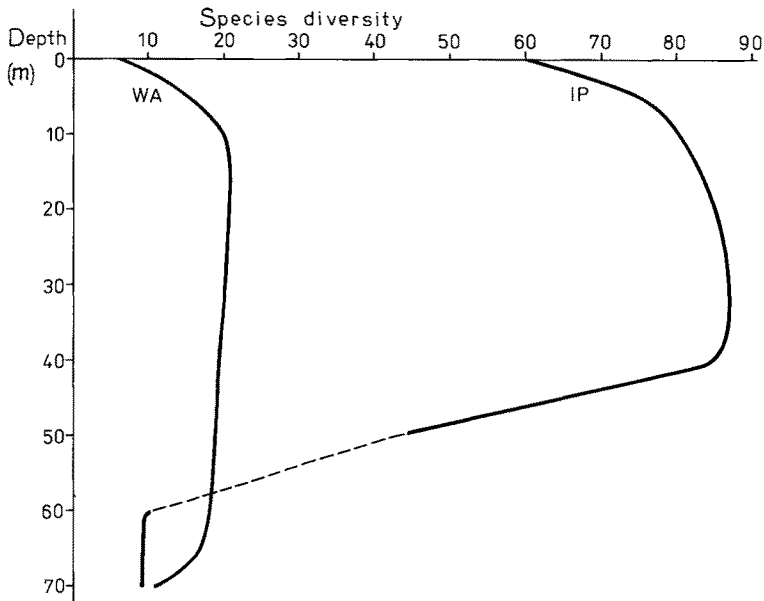


Fig. 3. Species diversity (number of species) of stony corals at different water depths in the West Atlantic (WA) and Indopacific Ocean (IP)



associations can occur despite equally balanced environmental conditions in the deep-water zone of the same reef, if there are different hydrodynamic conditions.

Steep, hard bottom substrates are particularly characteristic of the deep-water zone of coral reefs. Flat rocky substrates sand up quickly through sediment settling in calm water. Waterborne sediments were not permanent on the steep substrates on which these investigations were conducted because even slight water movement could easily stir them up and transport them to lower depths. When sediments are lacking, the water is rarely turbid in the vicinity of steep slopes and this is particularly favourable for coral growth. Moreover, the water is subjected to continuous exchange processes brought about by the slow currents usually occurring there. Thus, the following conclusion is drawn: steep slopes with an angle of inclination between 50 and 80° and at depths between 20 and 50 m are particularly suited for colonization by deep-water coral associations. The interaction and alteration of the environmental factors of hydrodynamics, substrate and sedimentation constitute a complex of mechanical factors acting in concert. It appears to be responsible for the formation of coral associations (Kühlmann, 1977) together with other controlling factors such as competition (Lang, 1971, 1973; Hildeman et al., 1975; Sheppard, 1982), conditions of settlement (Sammarco et al., 1974), predators (Salvini-Plawen, 1972; Collins, 1974, 1975; Harris, 1975; Frydl, 1979; Lauckner, 1980), population dynamics (Margalef, 1978) and others. Typical deep-water coral associations occurring in more shallow waters are exceptions due to altered conditions of mechanical factors. Coral growth appears to be impeded below 40 to 50 m because of cooler temperature, stronger sedimentation in calm water and greatly reduced light intensities. It is reduced in overhanging substrates because corals projecting too far into the water or becoming too heavy break off and fall into deeper zones.

Of the 92 coral species (one hydrocoral) in the Central Pacific and the Red Sea living below 20 m (Table 4), 74 of them occur above 5 m and 12 of them at depths between 5 m and 20 m (Fig. 3). Only 6 Scleractinia species were found exclusively below 20 m. Although this calculation is still based on incomplete data, as many as 80 % belong to species which exist in shallow as well as in medium-deep and deep-water zones of the reefs; 13 % occur in both medium-deep and deep-water ranges and a mere 7 % are found exclusively in deep-water zones. Of the 21 coral species (among them 1 hydrozoan) found in the Western Atlantic, in the deep water of the reefs of St. Croix and Cuba (Table 5), Goreau & Wells (1967), Wells (1973) and Zlatarski & Estrella (1982) attributed 18 species to shallow waters less than 5 m deep and 3 species to the medium-deep zone between 5 m and 20 m. Solely *Mycetophyllia reesi* has been found so far at depths between 27 and 76 m. Accordingly, 85 % of the corals are found in the deep-water zone and 14 % in the medium-deep zone, while less than 1 % live in the deep-water zone only (Fig. 3). Thus, depth zoning of hermatypic symbiotic coral species, growing between shallow water (< 5 m) and deep water (> 20 m) is not in conformity with the spectrum of light selectively absorbed by the water, but rather with hydrodynamics (Graus et al., 1977), sedimentation, surface condition, substrate inclination and other factors which change with increasing depth. The occurrence of some hermatypic corals exclusively in the deep-water zone may be attributed to mechanical conditions, light, other ecological factors and/or the genetically fixed property of forming only fragile skeletons.

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