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Coral Reefs

Light-dependence in scleractinian distribution in the sublittoral zone of South China Sea Islands

E. A. Titlyanov and Y. Y. Latypov

Institute of Marine Biology, Far East Branch, USSR Academy of Sciences, Vladivostok 690032, USSR

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Abstract. The distribution of 64 reef-building scleractinian species was studied in turbid waters of the South China Sea. The depth limit of scleractinian distribution in the Gulf of Siam is 18–20 m with 8–2% of incident surface irradiance, which is close to the lower light limit of most corals containing zooxanthellae. Forty percent of the scleractinian species studied inhabit the entire depth range with 70–30% of incident surface irradiance. No specific "grotto" species were identified even in sites of extreme shading, though only explanate plate, corymbose and encrusting colonies were found in low light levels.

Introduction

In recent years, observations using SCUBA and submersibles have shown that maximum depth for most hermatypic corals occurs at light levels between 2–0.5% of incident surface radiation (Yamazato 1972; Lang 1974; Falkowski and Dubinsky 1981; Titlyanov et al. 1981, 1983; Dustan 1985; Kühlmann 1982; Fricke and Schuhmacher 1983; Porter et al. 1984; Fricke and Meischner 1985). Few coral species appear to possess unique capabilities that enable them to adapt to light levels below this threshold.

Coral distribution at various depths (Kühlmann 1982; Fricke and Schuhmacher 1983; Fricke and Meischner 1985), and in open and shaded shallow sites (Pichon 1976; Dinesen 1982) showed that many species have a wide range of depth distribution.

Coral colonies often have a morphological change as a function of depth. This may facilitate maximal light absorption (Fricke and Schuhmacher 1983; Porter et al. 1984; Titlyanov 1987). Other selective advantages have also been attributed to the changes in colony shape that occur with increasing depth. Round, massive corals may be more resistant to wave energy in shallow water while flattened corals are less likely to roll down a steeply sloped reef face if their bases are damaged by boring sponges. Caribbean species with wide depth distributions are frequently polymorphic with massive or round colony shapes in shallow, well-lit habitats, and flattened or plate-like form in deeper water (Goreau 1959; Goreau and Wells 1967; Barnes 1973; Dustan 1975, 1979).

We report the distribution of corals with respect to depth and photic environments in the shallow water of the South China Sea and the Gulf of Siam. Ecological investigations were accompanied by field measurements of light intensity in coral habitats.

Area of study and methods

The investigation was carried out by a joint Soviet-Vietnamese expedition aboard the research vessel Akademik Nesmeyanov in the coastal zone of Anthoi, Thochu (Gulf of Siam) and Condao Islands (the South China Sea) (Fig. 1).

The vertical distribution of hermatypic corals was determined along transects placed perpendicular to the coastline from the intertidal zone down to the maximal depth in the site of survey. Species composition, quantitative distribution and abundance of scleractinian colonies were estimated using three to five 1 m^2 quadrats per meter of depth along the transect (Jokiel and Maragos 1978). Altogether, quadrats along 16 transects were studied (Fig. 1). Data from species common for all three islands and only individuals from open (unshaded) habitats are presented herein. Accordingly, the species subset consisted of 64 from a recorded total of 187 scleractinian species. To determine the light requirements of corals, 49 shaded bottom sites (niches, grottoes, caves of various shapes) were examined at the depths from 2 to 5 m along the coastlines of Anthoi, Thochu and Ba islands (Fig. 1).

The degree of depth-dependent irradiation was measured along the transects (Fig. 1) from the sea surface, in 2 m increments, to 20 m. Underwater light measurements were made by autonomous and cable irradiance meters. Both irradiance meters had silicon photodiodes with linear characteristics in a wide light range. A 300–740 μm-pass combined light filter was used. Thus, both instruments measured light energy were calibrated in W m^{-2}. Limits of light energy records by the instruments were 0.05 to 800 W m^{-2}. An autonomous irradiance meter was used to measure light levels in reef grottoes and niches. The degree of light reduction by the water column and daily dynamics of illumination in coral habitats were measured by a cable irradiance meter. When measuring a light energy value in cryptic coral habitat, the light collector was placed in the immediate proximity to the coral with the photodiode surface parallel to the best-illuminated colony surface. Irradiance values for shaded niches were measured every hour during the daylight with sensors oriented towards niche openings. In addition, light was measured on open bottom sites (at the depth of the shaded niches) and above the

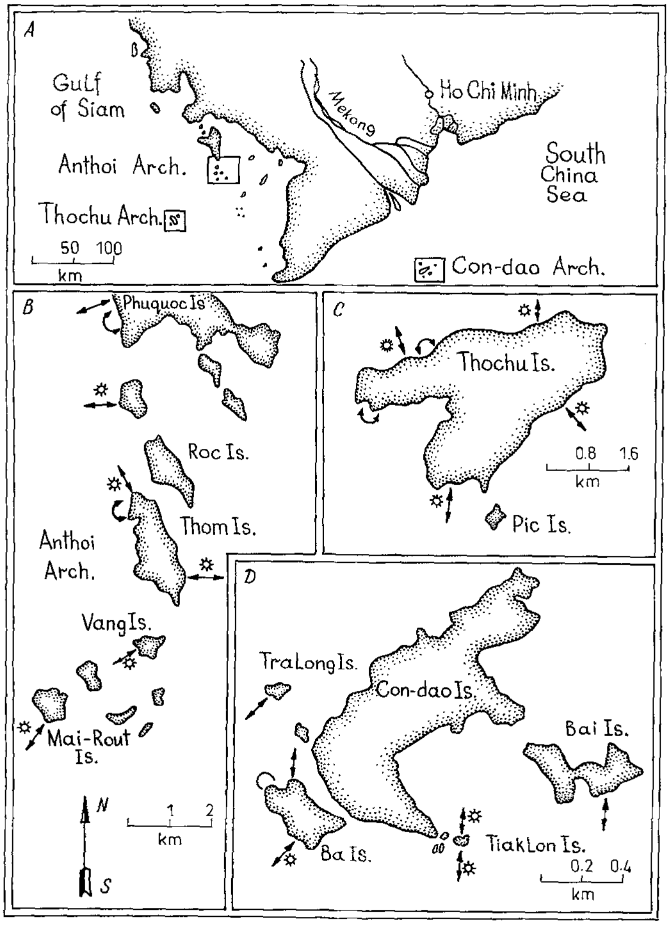

Fig. 1 A–D. Schematic maps of the area of study. **A** General scheme. **B** Anthoi Islands, 9°57′ N, 104°02′ E. **C** Thochu Islands, 9°18′ N, 103°28′ E. **D** Condao Islands, 8°40′ N, 106°38′ E. □ = investigated sites; ↔ = location of transects; ⌒ = shaded niches; ✲ = station for estimation of surface irradiance at different depths

water surface. Underwater light measurements were made from 10 to 11 a.m. and from 3 to 4 p.m.

Total solar radiation just above the water surface was continuously recorded daily with the use of a standard irradiance meter (Yanishevsky's pyranometer) used in the USSR for measurements of total solar irradiance. The amount of incident surface irradiance (350–710 µm) during a day was taken as 50% of the total incident solar radiation (Tooming and Gulyaev 1967). A correction for water surface reflection was applied: 3% in midday, 20% in the first and the last hours of day light and 10% in the second and penultimate hours of the day (Jerlov 1970). The light penetrating into different depths and shaded shallow water niches was expressed in percent of the surface irradiance.

Types of coastal water was defined in the areas studied, according to Jerlov's classification (Jerlov 1970). A light filter with maximal light admission at 545 µm was installed in the silicon-photodiode irradiance meter described above, and light energy was registered at two depths, z_1 and z_2. The values of light energy obtained for these depths, Iz_1 and Iz_2, were used to calculate coefficients of light attenuation (545 µm) by the water column according to the formula:

$$K=\frac{1}{z_2-z_1}\cdot\ln\frac{Iz_1}{Iz_2}$$

Measurements (10–15) at different depths were used to calculate the mean value for the coefficient K in a given water area. Using the coefficient of light attenuation in the region of 545 µm, coastal water types were identified according to the Jerlov classification (Jerlov 1970).

Results

Light regime in coral habitats

Shallow waters of the Anthoi, Thochu and Condao islands are turbid and may be classified as coastal water types 1 to 5 according to the Jerlov (1970) classification. The most transparent waters were found near the northeastern coast of Thochu Island (coastal type 1), and the Mai-Rout and Tralong Islands (coastal type 2). The turbid waters were in the vicinity of Thom and Ba Islands (coastal type 5) and at the southern coast of Thochu Island (costal type 4, Figs. 1 and 2). Water transparency decreased as the coastline was approached, with deeper sites having clearer water than more shallow sites (Table 1).

These data were used as the bases for an analysis of vertical distribution of Scleractinia with regard to light intensity (Table 2).

The irradiance level in cryptic habitats was strongly dependent on geographic orientation of a grotto or cave. Thus, cryptic habitats with an eastern opening received up to 10% of irradiance while levels at southern exposed openings were decreased to 6% of the available light. Eastern sites received the majority of their illumination during the early morning hours while southern niches were brightest in the afternoon hours. Exposure during these times accounted in the "eastern" niche for 20% and in the "southern" niche for 80% of the total daily irradiance.

Distribution of Scleractinia over depths and shaded reef niches

Up to 40% of 64 scleractinian species studied herein inhabited the entire depth range from 1 to 20 m at light from 90 to 2% of incident surface irradiance (Table 2), only 18% did not penetrate to 18–20 m (8–2% light), the greatest depths of distribution recorded for these areas.

Table 1. Depth-dependent variations of light value in the area of study. SI = surface irradiance; W = absolute light value in a fair afternoon

Locations	Light values at different depths									
	1–2 m		3–5 m		9–11 m		12–15 m		18–20 m	
	SI (%)	$W\,m^{-2}$	SI (%)	$W\,m^{-2}$	SI (%)	$W\,m^{-2}$	SI (%)	$W\,m^{-2}$	SI (%)	$W\,m^{-2}$
Anthoi Islands	83–39	348–163	43–18	180–76	18–8	76–36	10–5	42–21	8–2	34–4
Thochu Islands	89–59	373–248	67–23	281–97	39–18	163–76	30–10	126–42	9–8	38–34
Condao Islands	82–31	344–130	52–17	218–71	28–10	117–42	18–8	76–34	8–4	34–17
Averaged value for all islands	89–31	373–130	67–17	281–71	39–8	163–34	30–5	126–21	9–2	38–4

Table 2. Vertical distribution of scleractinians over open bottom sites near the Anthoi, Thochu, and Condao Islands. — = species not found; + = single individuals occurred (0.1 col. m^{-2}); × = rare occurrence (0.5–1 col. m^{-2}); c = common occurrence (3–5 col. m^{-2}); a = abundant occurrence (7–10 col. m^{-2}) up to continuous covering. Light ranges of coral habitats are averaged (see Table 1)

	Depth (m)				
	1–2	3–5	9–11	12–15	18–20
	Surface irradiance (%)				
	89–31	67–18	39–8	30–5	9–2
Psammocora contigua (Esper)	×	×	c	c	+
P. superficialis (Gardiner)	—	—	+	×	+
P. profundacella (Gardiner)	×	×	c	a	+
Pocillopora damicornis (Linn.)	o	a	a	o	×
P. verrucosa (Ellis and Solander)	o	a	a	o	×
Seriatopora hystrix (Dana)	×	o	a	×	+
Stylophora pistillata (Esper)	+	×	×	+	+
Madracis kirbyi Veron and Pichon	—	+	+	×	—
Montipora tuberculosa (Lam.)	×	c	c	c	+
M. spongodes Bernard	+	×	×	+	+
M. hispida (Dana)	+	a	c	×	—
M. aequituberculata Bernard	×	a	a	×	—
Acropora palifera (Lam.)	+	c	a	×	—
A. gemmifera (Brook)	c	c	×	×	—
A. nobilis (Dana)	+	a	c	×	—
Pavona cactus (Forskal)	+	a	a	×	+
P. decussata (Dana)	+	a	c	×	+
Leptoseris explanata Yabe and Sugigama	—	—	+	c	×
Gardinoseris planulata (Dana)	—	—	×	×	+
Pachyseris rugosa (Lam.)	—	+	a	c	c
Coscinaraea exesa (Dana)	—	—	×	c	×
Cycloseris cyclolites (Lam.)	—	—	—	×	a
C. patelliformis Boschma	—	—	—	+	c
Fungia paumotensis (Stutch.)	—	+	×	c	c
Podobacia crustacea (Pallas)	—	+	×	c	×
Galaxea astreata (Lam.)	—	×	×	×	—
G. fascicularis (Linn.)	×	c	a	c	+
Merulina ampliata (Ellis and Solander)	—	—	×	c	+
Scolymia vitiensis (Brugg.)	—	—	—	×	+
Lobophyllia hemprichii (Ehrenberg)	+	×	c	c	+
L. hataii (Yabe, Sugigama and Eg.)	+	×	c	c	+
Mycedium elephantotus (Pallas)	—	×	×	c	+
Pectinata lactuca (Pallas)	—	—	×	c	+
P. paeonia (Dana)	—	—	+	c	+
Euphyllia glabrescens (Spengler)	—	+	×	c	+
Plerogyra sinuosa (Dana)	—	+	c	c	+
Physogyra lichtensteini (M.E. and H.)	—	—	×	×	—
Porites australiensis Vaughan	a	a	c	c	+
P. lutea (M.E. and H.)	c	a	c	c	+
P. cylindrica (Dana)	c	a	c	×	+
P. rus (Forskal)	a	a	c	×	×
Goniopora djiboutiensis Vaughan	—	+	×	a	c
G. stokesi (M.E. and H.)	+	×	c	a	c
Alveopora spongiosa (Dana)	—	+	c	a	c
Favia stelligera (Dana)	×	c	c	c	+
F. speciosa (Dana)	×	c	c	c	×
F. maxima Veron and Pichon	—	+	×	×	+
Favites abdita (Ellis and Solander)	c	c	c	c	×
Goniastrea retiformis (Lam.)	a	c	c	c	×
G. pectinata (Ehrenberg)	a	c	c	c	×
Platygyra daedalea (Ellis and Solander)	c	a	a	c	+
Leptoria phrygia (Ellis and Solander)	×	a	a	c	—
Plesiastrea versipora (Lam.)	—	—	×	c	×
Leptastrea purpurea (Dana)	×	×	c	a	c
L. transversa Klunzinger	×	×	c	a	c
L. bewickensis Ver., Pich. and W.B.	—	—	—	×	+
Cyphastrea serailia (Forskal)	×	c	c	×	+
C. microphthalma (Lam.)	×	c	c	c	+
Echinopora lamellosa (Esper)	—	×	×	c	×
Trachyphyllia geoffroyi (Audoin)	—	—	—	c	×
Turbinaria peltata (Esper)	+	×	c	a	c
T. mesenterina (Lam.)	—	×	a	a	+
T. radicalis Bernard	—	—	×	×	+
Tubastrea micranta (Ehrenberg)	—	+	c	c	+

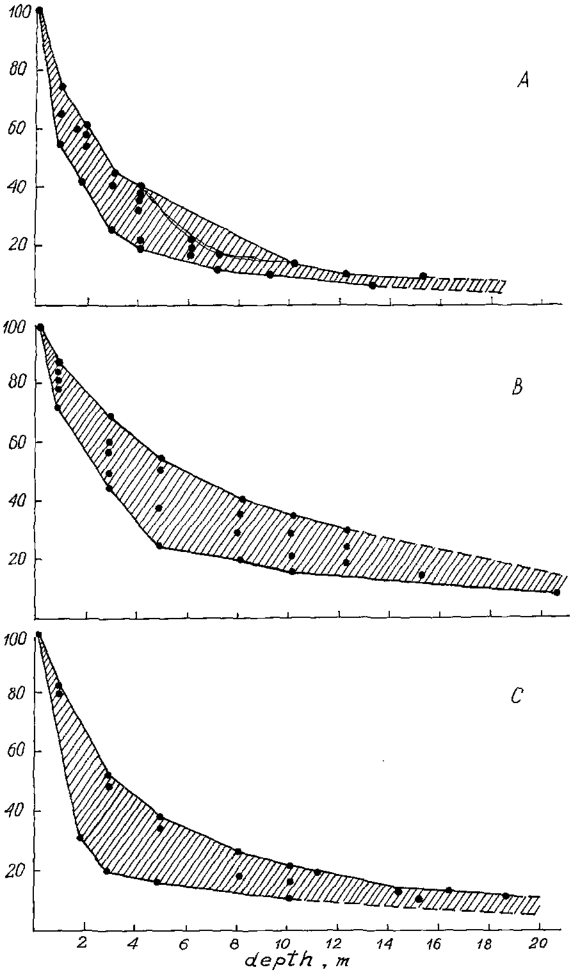

Fig. 2 A–C. Light value at different depths (in % to surface irradiance). A Anthoi Islands (Thom, Roi, Vang, Mai-Rut). B Thochu Islands. C Condao Islands (Tralong and Ba)

Scleractinians were rare in the intertidal zone and in the first meter of the upper sublittoral zone, they were more often found in shallow sites protected from direct wave action. *Pocillopora verrucosa, Porites australiensis, P. rus, Goniastrea retiformis* and *G. pectinata* colonies found down to 1 m were poorly developed and included many dead colonies (Fig. 3). Specialized shallow water species were not found. *Cycloseris cyclolites, C. patelliformis, Scolymia vitiensis, Leptastrea bewickensis* and *Trachyphyllia geoffroyi* occurred only deeper than 12 m, and only *C. cyclolites* was abundant at depths greater than 18 m.

The species found at each depth gradually increased from 52 to 100% of the total pool from 1 to 15 m (90–10% light), and fell again to 82% only at maximal depths of 18–20 m (8–2% light) (Table 2). At moderate depths of 5 to 15 m, relative frequency of abundant and common species increased up to 28 and 48% respectively. At the same time, the relative numbers of abundant and common species fell at maximal depths to 2 and 4%, respectively (Table 2). The relative frequency of occurrence for single colonies of rare species declined with increasing depth (to 3% at 15 m depth) and then abruptly increased (by up to 59%) at the maximum site depth (Table 2).

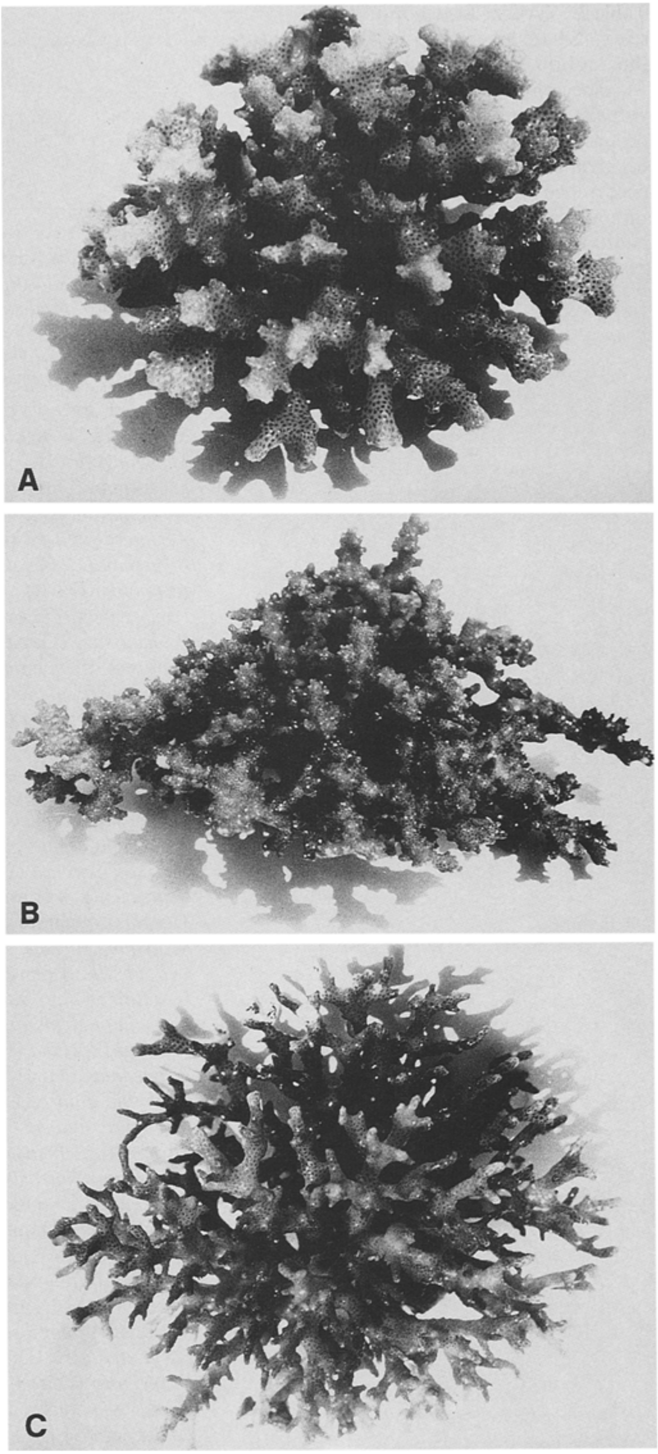

Fig. 3 A–C. *Pocillopora damicornis* colonies from habitats of different illumination. A 1.5 m depth, open site, 80% of surface irradiance. B 2 m depth, shaded niche, 5% of surface irradiance. C 18 m depth, open site (10% light)

Scleractinians in deep waters showed mainly explanate plate, corymbose and encrusting colony forms, as in the species *Coscinarea exesa, Cycloseris cyclolites, Gardinoseris planulata, Leptastrea bewickensis, Leptoseris explanata, Merulina ampliata, Pectinata lactuca, P. paeonia, Psammocora superficialis*. However numerous branched scleractinian corals (*Pocillopora damicornis, P. verrucosa, Seriatopora hystrix*) and massive colonies (*Lobophyllia hemprichii, L. hataii, Porites australiensis* and *Platygyra daedalia*) also occurred at maximum depth.

In coastal shallow waters, the lowest irradiation in shaded niches and rock grottoes in 6 times lower than

Table 3. Lower light limit of scleractinian distribution in rock grottoes and niches (occurrence of "shade" species in open bottom sites – see Table 2)

Scleractinian species	Light value in colony habitat in the fair afternoon	
	Surface irradiance (%)	W m^{-2}
Porites lichen (Dana)	0.3–1	1.3– 4.2
Porites australiensis Vaughan	0.3	1.3
Favites abdita (Ellis and Solander)	0.3–7	1.3–29
Alveopora spongiosa (Dana)	0.4–7	1.7–29
Favia stelligera (Dana)	0.4–9	1.7–38
Pavona decussata (Dana)	0.5–8	2.1–34
Leptastrea bewickensis Veron	0.5	2.1
Turbinaria mesenterina (Lam.)	0.6–2	2.5– 8.4
T. radicalis Bernard	0.7–2.2	2.9– 9.2
T. retiformis Bernard	0.8	3.4
Podobacia crustacea (Pallas)	8	3.4
Lobophyllia hataii (Yabe, Sugigama and Eguchi)	0.9–8	3.8–34
Favia maxima Veron	1 –1.5	4.2–63
Pocillopora damicornis (Linn.)	1.6–8	6.7–34
Platygyra lamellina (Ehrenberg)	2	8.4
Pocillopora verrucosa (Ellis and Solander)	3 –7	13 –29
Galaxea astreata (Lam.)	7	29
Platygyra daedalea (Ellis and Solander)	8	34
Lobophyllia hemprichii (Ehrenberg)	8	34
Madracis kirbyi Veron and Pichon	9	38

that of its vertical depth limit, and consists of 0.3% of incident surface irradiation or 1.3 W m^{-2} in the cloud-free afternoon (Table 3). Twelve scleractinian species occur in shaded habitats at an irradiation of less than 1% of incident surface irradiation. 15 of 20 scleractinian species found on strongly shaded niches were also found at maximal depth of coral distribution. *Alveopora spongiosa* inhabiting niches at 0.4% of light was a common species at depths of 18–20 m. Species which were recorded in shaded habitats occurred also in open shallow waters (15 to 20 species). All colonies sampled in niches and grottoes at an irradiation lower than 1% of incident surface irradiation were encrusting or explanate.

Discussion

The distribution of hermatypic corals over depths and shaded reef niches has been studied mostly in oceanic regions with transparent waters of oceanic types (Jerlov 1970) I and II in terms of transparency (Yamazato 1972; Pichon 1976; Dinesen 1982; Kühlmann 1982; Fricke and Schuhmacher 1983; Fricke and Meischner 1985). In turbid waters of the Gulf of Siam coral distribution is "compressed" within the range from 0 to 20 m. Despite a "compressed" reef and optical heterogeneity of waters, we have established some light-dependent regularities in vertical distribution of hermatypic corals. In the Gulf of Siam, scleractinians occur down to 18–20 m, the maximal depth for the region. Irradiance in these depths is 8–2% of surface irradiance, which is close to the light limit in habitats of major coral species containing zooxanthellae.

Another distinctive feature of coral reefs in the Gulf of Siam is a nearly complete absence of scleractinians in the intertidal zone and over the first few dozen centimeters of the sublittoral zone. Only a few isolated colonies of *Porites* species could be found in the intertidal zone of a wave-protected reef flat, and *Pocillopora verrucosa* occurred in shaded and wave-protected sites of rocky coasts. The upper limit for scleractinian growth in the Gulf of Siam is not determined by inhibition due to full solar irradiation. We believe that survival of scleractinians at zero depth is limited by a number of environmental factors other than visible light. Some recent works on scleractinian coral distribution show that such environmental factors as wave action, strong sedimentation, and moving sand substrate may be critical to the survival of corals in shallow waters (Fricke and Meischner 1985; Sakai et al. 1986).

Species richness of corals inhabiting evenly irradiated bottom sites increased with depths and decreased again only at maximal depths. It is very likely that an increase of scleractinian species diversity with depth in the Gulf of Siam is caused by a complex of factors. Light within 80 to 15% of incident surface radiation did not limit the existence of a majority of scleractinian species. Earlier, we had established that most species of reef building corals in the irradiation range of 80 to 10% of surface irradiance retain a stable level of total photosynthetic productivity which sharply drops only at greater levels of shading (Titlyanov et al. 1988). Major coral species enjoy favourable conditions at moderate depths. However, at moderate depths with irradiance of 80 to 10% of surface irradiance, maximal number of species concentrated near the lower limit of the range (30–10% of light). Such distribution seems to be associated with an intensive growth of competitive scleractinian species at irradiance of 80 to 30% of surface light. With a decrease in irradiance to 30–40% of surface light, abundant earlier successional species lose their advantage and other more competitive corals occupy the free substrate. This suggestion is supported by evidence that abundant species with well-developed colonies are more frequent in occurrence at irradiance of 70 to 30% of surface light and that the relative frequencies of rare species with small colonies increases at irradiance of less than 30% of surface light (Table 2).

Forty percent of scleractinian species occur over the entire depth range on evenly irradiated bottom sites. Similar results (25–35% of species) were obtained for Polynesian islands, Jamaica and Cuba (Kühlmann 1982). We did not find any photophilous scleractinian species (only at bright light) or any references in the recent literature of their existence in other regions of the World Ocean (Pichon 1976; Kühlmann 1982; Fricke and Schuhmacher 1983; Fricke and Meischner 1985; Sakai et al. 1986). Only 8% of the coral species investigated, which occur at irradiance less than 30% of surface light, might be considered as typical skiophilous species: *Cycloseris cyclolites, C. patelliformis, Scolymia vitiensis, Leptastrea bewickensis* and *Trachyphyllia geoffroyi.*

In the Gulf of Siam, corals of several genera dwell in caves with 0.3% of surface irradiance during the most of the day. This irradiance may be optimal for some algal species, as, for example, calcareous red algae of the genus *Lithothamnion,* which dwell at 0.1–0.05% of surface irradiance (Molinier 1960; Lang 1974). Littler et al. (1986) found photosynthetically competent non-articulated coralline abundant at 0.0005% of the surface irradiance in the Bahamas. Fricke and Meischner (1985) also note a considerably greater shade tolerance of algae in comparison with corals for the Bermuda Islands where communities of hermatypic corals at the depth of 70 m (5% of light) changed to macroalgal communities.

Shaded niches and grottoes are inhabited by scleractinian species which are also widely represented on illuminated bottom sites and at maximum depths. We did not find specific "grotto" species. Similar results were also obtained on Australian reefs (Pichon 1976; Dinesen 1982) and the Bermudas (Fricke and Meischner 1985). But Pichon distinguished three groups of hermatypic corals dwelling in shaded habitats: generally skiophilous corals found both in deep and in shallow waters, but under shaded conditions; preferentially cavernicolous corals growing mostly in shallow cryptic habitats; and shade-tolerant corals common also in better-illuminated parts of the reef, but tolerant of a wide range of illumination conditions (open shallow waters, grottoes and deep waters). In the Gulf of Siam and Condao islands, we distinguished only two scleractinian groups in relation to light conditions in their habitat: 1) skiophilous species (8% of the total number) inhabiting only great depths (from 30 to 2% of surface irradiance); and 2) shade-tolerant species (64% of the total number) dwelling in a wide range of irradiance (from 70 to 2% of surface irradiance).

Studies on the distribution of coral growth forms (Goreau 1959; Dustan 1975; Jaubert 1981; Fricke and Schuhmacher 1983; Fricke and Meischner 1985; Titlyanov 1987) have indicated that a decrease in light intensity with depth or shading coincides with flattening of coral colonies. Our records confirmed the earlier observations in general but also showed that extremely shaded grottoes and niches in the Gulf of Siam are inhabited only by encrusting and explanate plate forms of corals.

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