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Light Adaptation and Production Characteristics of Branches Differing by Age and Illumination of the Hermatypic Coral *Pocillopora verrucosa*

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Abstract

The *in situ* irradiance of different parts of the coral colonies of *Pocillopora verrucosa* (Ell. et Sol.), the morphology of branches of the different growth order, and their productivity were investigated in the Gulf of Siam. Irradiances of different parts of the colony varied more than 50-fold. Self-shading of inner sections of the colony was particularly significant in specimens in high light habitats. Younger coral branches had higher polyp concentrations, larger polyp size, higher zooxanthellae content, and higher photosynthetic capacity. Branches of the three investigated orders adapted to low light intensity of their habitat, keeping their photosynthetic capacities at illumination decrease from 90 to 30% PAR on surface. Main mechanisms of coral colony adaptation to low light are maximization of uptake and efficient utilization of absorbed light. The result of coral adaptation to light intensity decrease in a habitat is a high and relatively stable level of primary production in a wide light range.

Keywords: *Pocillopora verrucosa*, zooxanthellae, light adaptation

1. Introduction

Adaptation of hermatypic coral species to lower light intensities has been attributed to: (1) an increase in photosynthetic pigment content of zooxanthellae (Titlyanov et al., 1978, Falkowski and Dubinsky, 1981; Porter, et al., 1984), (2) an increase in size of photosynthetic units (Leletkin et al., 1980; Falkowski and Dubinsky, 1981), (3) increased concentrations of phtosynthetic

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membranes in the chloroplast (Dubinsky et al., 1984), (4) an increased zooxanthellae density per unit area of coral surface (Titlyanov et al., 1980; Kinzie and Hunter, 1987), and (5) morphological changes of coral colonies (Fricke and Schuhmacher, 1983; Titlyanov, 1987). We believe this list is incomplete. There is little information on adaptive reactions of corals to differences in light intensity and quality (Kinzie and Hunter, 1987) and illumination ranges of coral habitats. Furthermore, no studies have been made on growth order (age) dependence of the adaptive reactions.

In this paper we examine productivity characteristics of corals collected from different light conditions. The experiments were designated with the following specific objectives: to evaluate the effect of coral growth order on adaptation to light and to analyse autotrophic productivity characteristics of coral colonies over the entire light range of coral habitats.

2. Materials and Methods

Coral distribution

We investigated the reef-building branching coral *Pocillopora verrucosa* (Ell. et Sol.). The work was carried out in the Gulf if Siam near the Fukuoq, Anthoi and Thochu islands. Corals for analysis were collected over the entire range of coral growth.

Sampling

Without removing coral samples from water, they were transferred to a tank of seawater and transported to the vessel within an hour of collection. Aboard the ship, coral samples were kept in aquaria with biological filters and aeration at light conditions similar to irradiance in their habitats. Samples were analysed the following day.

Photosynthetically active radiance (PAR)

For PAR measurements under water we used a specially constructed irradiance meter with a silicon photodiode (Titlyanov et al., 1988a). The instrument measured light energy close to PAR and was calibrated in $W \cdot m^{-2}$. Total incident surface solar radiation was continuously recorded by a surface irradiance meter. Incident surface PAR during a day was taken as 50% of the total incident solar radiation (Tooming and Gulyaev, 1967; Titlyanov et al., 1988a). In the experiments, the PAR penetrating the water to a selected depth at any time of the day was calculated both in energy units ($W \cdot m^{-2}$) and in percent of surface irradiance using the value of PAR reduction by the water column.

Light distribution within coral colonies was measured by a silicon mini-photodiode (Titlyanov et al., 1988b).

Colony surface area, polyp concentration, isolation of zooxanthellae and estimation of their amount in corals

Coral colony surface area occupied by polyps was measured by wrapping dry coral pieces with thin aluminium foil, and the total area was calculated (Marsh, 1970). Isolation of zooxanthellae and estimation of their amount in corals was made with the help of the methods described earlier (Zvalinsky et al., 1978).

Chlorophyll a *and* c_2 *concentrations in zooxanthellae*

These were estimated using the methods and equations of Jeffrey and Humphrey (1985).

Light dependence of the rate of coral photosynthesis

Light dependence was determined polarographically in small coral pieces (5–8 polyps) (Titlyanov et al., 1988b). In our measurements we used a polarographic cell (exposure chamber) constructed by V.A. Leletkin (1978).

Light curves of gross photosynthesis

Light curves measured in units of ampermeter readings were calculated in $\mu g\ O_2 \cdot cm^{-2}$ (of coral surface area) h^{-1}, as it was described earlier (Titlyanov et al., 1988b). For this, we measured the rate of gross photosynthesis at light saturation using Winkler's method (Sirenko, 1975) and at the same time measuring P vs I curve, according to Chalker et al. (1983), who measured the following parameters of the P vs I curve:

- the initial slope of the curve (α), showing the intensity of utilization of low light by corals;
- the light intensity at which the initial slope of the curve intercepts the horizontal asymptote (I_k);
- gross photosynthetic rate at saturating light intensity (P_s).

Estimation of net photosynthesis and dark respiration of different colony parts

Measurements of photosynthesis and dark respiration were carried out on branches of different age as shown in Fig. 1. With photosynthetic light curves

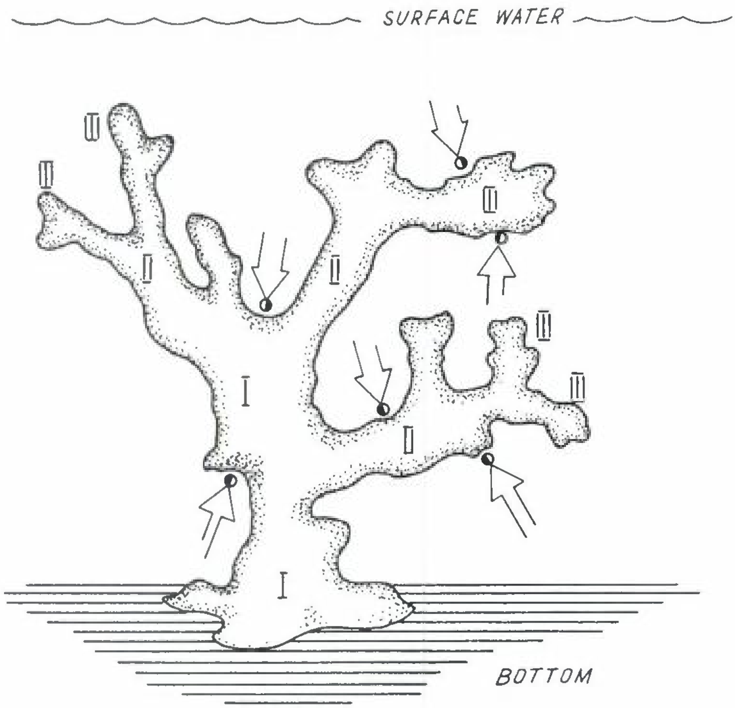

Figure 1. Arrangement of the I, II and III-order branches in *P. verrucosa* colonies and the position of light sensors among the branches of a colony.

and the I_k value determined in coral pieces of III, II and I growth orders, net photosynthesis rate at saturating light intensity was measured in the same or neighbouring coral branches. For estimation of net photosynthesis rate, we used the vessel method of chemical determination of oxygen, evolved at photosynthesis — Winkler's Method (Sirenko, 1975; Titlyanov et al., 1988b). The same method was used for determination of respiration rate in the dark.

Gross photosynthesis rates were calculated from experimental data as the sum of oxygen evolution rate in net photosynthesis and the oxygen uptake rate in dark respiration. Photosynthetic production of III, II and I order branches under natural light conditions was calculated from measurements of photosynthetic light curves, photosynthetic capacities of coral branches at saturating light intensity and natural illumination of colony branches.

3. Results

Light within a coral colony

Colonies were illuminated very unevenly due to self-shading by their own upper branches (Fig. 1, Table 1). On a sunny midday in February in the Gulf of Siam, natural illumination of different colony parts of *P. verrucosa* exposed to 90, 60 and 5% PAR on surface ranged from 380 to $8 W \cdot m^{-2}$, from 230 to $8 W \cdot m^{-2}$ and from 21 to $0.6 W \cdot m^{-2}$, respectively.

Morphological characteristics of coral colonies

Of all measured and calculated morphological characteristics of coral colonies (Table 2), the ratio of the bottom area covered by colony projection (parallel colony projection to bottom) to colony mass varied most widely. The ratio increased more than twice with illumination attenuation in the coral habitat from 70 to 5% of PAR on surface.

With lower illumination in the coral habitat, colony weight was reduced (Table 2) and morphology became considerably flattened. This was evident in the increase of the ratio of their maximum diameter to their maximum

Table 1. Light distribution within *Pocillopora verrucosa* colonies from different habitats. Numerator is the value for the upper illuminated branch side and denominator is the value for the lower shaded branch side (Fig. 1). Values are means and standard deviations of 3 to 5 measurements of different coral colonies.

Type of habitat	Depth (m)	% PAR on surface	Illumination of orders of branches**			Light energy for orders of branches at midday ($W \cdot m^{-2}$)		
			III	II	I	III	II	I
Illuminated shallow waters	1	90	$\frac{100}{24}$	$\frac{18}{6}$	$\frac{10}{2}$	$\frac{380}{91 \pm 34}$	$\frac{70 \pm 21}{23 \pm 12}$	$\frac{38 \pm 14}{8 \pm 4}$
Shadow	1	60	$\frac{100}{14}$	$\frac{41}{12}$	$\frac{23}{7}$	$\frac{230}{32 \pm 7}$	$\frac{94 \pm 31}{28 \pm 16}$	$\frac{53 \pm 41}{8 \pm 7}$
Shadow*	2	30	$\frac{100}{30}$	$\frac{21}{6}$	$\frac{18}{5}$	$\frac{126}{38 \pm 8}$	$\frac{26 \pm 9}{8 \pm 2}$	$\frac{23 \pm 7}{6 \pm 1}$
Extreme shading	1	5	$\frac{100}{11}$	$\frac{41}{24}$	$\frac{15}{3}$	$\frac{21}{2 \pm 1}$	$\frac{9 \pm 3}{5 \pm 3}$	$\frac{3 \pm 2}{0.6 \pm 0.1}$

* Light distribution in colonies of the coral *Pocillopora damicornis* — the species similar to *P. verrucosa* by its morphology and adaptive reactions.

**(PAR in % of PAR on surface in the habitat)

Table 2. Morphological characteristics of *P. verrucosa* colonies from various habitats. Values are means and standard deviation of 5 to 15 measurements of different coral colonies

Light conditions	Depth (m)	% PAR_s	Dry weight of coral colony (g)	Ratio of projection of colony to weight (cm g^{-1})	Number of polyps per 1 cm^2 of coral surface			Diameter of polyps (mm)		
					III order	II	I	III order	II	I
Light	1	90	318±58	0.36±0.03	102±2	89±4	86±2	0.88±0.04	0.83±0.08	0.74±0.05
Light	4	70	304±94	0.23±0.03	103±2	93±2	83±2	1.00±0.03	0.98±0.02	0.82±0.04
Light	7	30	356±39	0.35±0.01	100±2	84±2	74±3	0.98±0.01	0.85±0.03	0.80±0.03
Light	14	10	203±7	0.50±0.01	98±2	94±7	89±4	1.00±0.03	0.90±0.02	0.89±0.03
Shadow	1.5	5	209±52	0.51±0.02	102±2	89±2	83±9	0.93±0.05	0.88±0.04	0.70±0.02

weight. Polyp concentration and their size increased mostly from the first order branches to the third order ones (Table 2).

Zooxanthellae density in *P. verrucosa* colonies decreased from branches of the III-order to those of the I-order in practically all colonies examined (Table 3). Zooxanthellae content in coral colonies increased with colony shading down to the level of 10% PAR and then in the III-order branches dropped with further light attenuation.

Chlorophyll a *contents in isolated zooxanthellae*

Chlorophyll *a* content in zooxanthellae depended on coral habitat (Table 3). On an average, zooxanthellae of III and II order branches of corals from the illumination range of 10–5% of PAR on surface had 1.5–2.5 times more chlorophyll than in the illumination range of 90–70% PAR on surface.

Chlorophyll c_2 content was on the average about 50% of chlorophyll *a* for all coral samples. Depending on illumination in a coral habitat, chlorophyll c_2 content in zooxanthellae varied similarly to that of chlorophyll *a*.

Light dependence of gross photosynthesis

The rate of gross photosynthesis at light saturation (P_s) decreased from the III to the I-order branches (Table 4). At the III and II-order branches, photosynthetic rate at light saturation considerably increased if habitat illumination decreased from 90 to 30% PAR on surface. But with a further decrease of illumination to 5% of PAR on surface, photosynthetic capacities dropped sharply.

In colonies inhabiting shallow waters at high illumination (90% PAR on surface), the slope of the linear region of the light curve (α), expressing photosynthetic efficiency at low light increased from the III to the I-order branches (Table 4). Light intensity for photosynthesis saturation (I_k) was about 120–140$W \cdot m^{-2}$ for the III-order branches, about 80–100$W \cdot m^{-2}$ for the II and 30–60$W \cdot m^{-2}$ only for the I-order branches.

With decrease in irradiance of a coral habitat to 60 and 30% of PAR on surface, efficiency of utilization of low light (α) for the III and II-order branches increased, and light saturation of photosynthesis decreased to 40–60$W \cdot m^{-2}$. Extreme shading conditions (10–5% of PAR on surface) caused loss of efficiency of utilization of weak light, especially in the I-order branches.

Table 3. Physiological characteristics of the III, II and I-order branches of *P. verrucosa* and their zooxanthellae in different habitats. Values are means and standard deviation of 3 samples from different coral colonies (for chlorophyll content — only 2).

Light conditions	Depth (m)	% PAR on surface	Zooxanthellae density on surface area (10^6 cells cm^{-2})			Chlorophyll *a* in zooxanthellae cells (μg per 10^6 cells)			Gross production of branches in their habitat in fair midday (μg O_2 $cm^{-2}h^{-1}$)		
			III order	II	I	III order	II	I	III order	II	I
Light	1	90	0.9±0.1	0.4±0.1	0.3±0.1	1.8	4.6	6.3	20±1.2	19.9±1.3	8.7±0.4
Light	4	70	1.5±0.2	0.7±0.1	0.8±0.1	2.2	4.1	3.1	–	–	–
Shadow	1.5	60	–	–	–	–	–	–	30±0.7	18.6±0.6	7.2±1.0
Light	7	30	–	–	–	11.9	9.1	10.0	36±1.0	18.2±1.3	7.1±0.5
Light	14	10	2.4±0.3	0.7±0.1	1.4±0.1	4.0	5.5	6.6	–	–	–
Shadow	1.5	5	1.3±0.1	0.8±0.1	1.5±0.1	7.7	5.8	5.3	10±0.3	5.4±0.4	1.4±0.3

Table 4. Light dependence of gross photosynthetic rate in the III, II and I-order branches of *P. verrucosa* in different habitats. Values are means and standard deviations of 3 samples from different coral colonies

Light conditions	Depth (m)	% PAR on surface	P_s, gross photosynthesis at saturating light intensity			I_k, saturating light ($W \cdot m^{-2}$)			α, initial slope of the light curve $\left(\frac{\mu g\ O_2\ cm^{-2}\ h^{-1}}{W \cdot m^{-2}}\right)$		
			III order	II	I	III order	II	I	III order	II	I
Light	1	90	20±1.2	19.9±1.3	16.1±0.6	120–140	80–100	30–60	0.25	0.25	0.40
Shadow	1.5	60	30±0.7	18.6±0.7	14.6±1.1	50–80	50–70	60–90	0.45	0.35	0.25
Light	7	30	36±1.0	26.1±2.3	23.1±1.9	40–60	40–60	40–70	0.60	0.70	0.50
Shadow	1.5	5	17±0.5	14.6±1.1	9.4±0.3	40–60	30–50	40–60	0.25	0.30	0.15

Photosynthetic capacity

Results on gross photosynthetic O_2 production of coral branches under natural illumination, taking into account self-shading inside a colony (Table 1), are presented in Table 4. It shows the maximal production for the III-order branches in the mid range of light (60–30% PAR on surface). Photosynthetic production generally decreased from the III-order to the I-order branches. In habitats of 90 to 30% of PAR on surface, all branches did not decrease their photosynthetic production in the middle of a fair day. At light attenuation to 5% PAR on surface, photosynthetic production dropped approximately 3-fold in the III-order branches, 3.5-fold in the II-order branches and 10-fold in the I-order branches from a light site.

4. Discussion

The data show that inner shaded colony parts of the coral *P. verrucosa* received 5–10 times less light than outer branches, and downward facing I-order surfaces received 15–20 times less light than upward III-order branches. Maximal self-shading of colonies was observed in highly illuminated shallow waters, and minimal self-shading at great depths or in shaded habitats. With illumination decrease, a branched colony of *P. verrucosa* flattened, and occupied larger bottom area (per coral weight unit) than colonies from highly illuminated shallow waters. Similar adaptive reactions were observed earlier in the branched coral *Stylophora pistillata* (Titlyanov, 1987).

It was shown, that irrespective of illumination, polyp concentration and corallite size decreased in order parts of I-order branches. In previous studies we suggested the possibility of some increase in polyp concentration on the outer surfaces of the III-order branches in *P. verrucosa*, *P. damicornis* and *Stylophora pistillata* at light intensity less than 10% PAR on surface (Titlyanov, 1987). In most cases zooxanthellae concentration also decreased in older branches. In some cases, chlorophyll content of the I-order branches dropped as compared with the III-order branches. Potential photosynthetic capacities of coral branches also decreased from younger to older ones.

All colony parts irrespective of their growth order showed the same adaptive responses to light attenuation: chlorophyll accumulation in zooxanthellae, increase of zooxanthellae concentration in polyp tissues, higher efficiency of assimilation of either weak or intensive (photosynthesis saturation) light. These adaptations to low light were first described for outer regular illuminated branches of different branched coral species (Titlyanov et al., 1978;

Zvalinsky et al., 1978; Titlyanov et al., 1980) and then confirmed for massive and branched species (Falkowski and Dubinsky, 1981; Porter et al., 1984; McCloskey and Muscatine, 1984).

We showed that photosynthetic rates of corals increased in low light down to about 30% of PAR on surface. It is probably connected with the accumulation of zooxanthellae in polyp tissues within this light range.

Calculations of gross productivity for coral branches of different growth order showed that branches of the coral *P. verrucosa* do not decrease primary production levels in the illumination range of 90 to 30% PAR on surface. This relatively stable primary production over a broad illumination range results from the coral adaptation to changing light intensity.

REFERENCES

Chalker, B.E., Dunlap, W.C., and Oliver, J.K. 1983. Bathymetric adaptations of reef-building corals at Davies reef, Great Barrier Reef, Australia. II. Light saturation curves for photosynthesis and respiration. *J. Exp. Mar. Biol. Ecol.* **73:** 37–56.

Dubinsky, Z., Falkowski, P.G., Porter, I.W., and Muscatine, L. 1984. Absorption and utilization of radiant energy by light- and shade-adapted colonies of hermatypic coral *Stylophora pistillata*. *Proc. Royal Soc. Lond. B* **222:** 203–214.

Falkowski, P.G. and Dubinsky, Z. 1981. Light-shade adaptation of *Stylophora pistillata*, a hermatypic coral from the Gulf of Eilat. *Nature* **289:** 172–174.

Fricke, H. and Schuhmacher, H. 1983. The depth limits of Red Sea stony corals: an ecophysiological problem (a deep diving survey by submersible). *PSZN Mar. Ecol.* **4:** 163–194.

Jeffrey, S.W. and Humphrey, G.P. 1975. New spectrophotometric equation for determining chlorophyll a, b, and c_1 and c_2 in higher plants, algae and natural phytoplankton. *Biochem. Physiol. Pflanz.* **167:** 191–194.

Kinzie, R.A., III and Hunter, T. 1987. Effects of light quality on photosynthesis of the reef coral *Montipora verrucosa*. *Mar. Biol.* **94:** 95–109.

Leletkin, V.A. 1978. Installation for measuring spectra and kinetic characteristics of photosynthetic evolution of oxygen by marine algae. In: *Ecological Aspects of Photosynthesis of Marine Macroalgae.* E.A. Titlyanov and V.I. Zvalinsky, eds. Far East Science Center, USSR Ac. Sci., Vladivostok, pp. 55–63.

Leletkin, V.A., Zvalinsky, V.I., and Titlyanov, E.A. 1980. Phtosynthesis of zooxanthellae of corals from different depths. *Physiology of Plants (USSR)* **27:** 1163–1170.

Marsh, J.A. 1970. Primary productivity of reef-building calcareous red algae. *Ecology* **51:** 255–263.

McCloskey, L.R. and Muscatine, L. 1984. Production and respiration in the Red Sea coral *Stylophora pistillata* as a function of depth. *Proc. Royal Soc. Lond. B* **222:** 215–230.

Porter, J.W., Muscatine, L., Dubinsky, Z., and Falkowski, P.G. 1984. Primary production and photoadaptation in light- and shade-adapted colonies of the symbiotic coral *Stylophora pistillata. Proc. Royal Soc. Lond. B* **222:** 161–180.

Sirenko, L.A. 1975. *Methods of Physiological and Biochemical Investigations of Algae in Hydrobiological Practice.* Naukova Dumka, Kiev. 247 pp.

Titlyanov, E.A. 1987. Structural-morphological differences of reef-building branched coral colonies from habitats of different illumination. *Marine Biology (Vladivostok)* **1:** 32–36.

Titlyanov, E.A., Shaposhnikova, M.G., and Zvalinsky, V.I. 1980. Photosynthesis and adaptation of corals to irradiance. 1. Contents and native state of photosynthetic pigments in symbiotic macroalgae. *Photosynthetica* **14:** 413–421.

Titlyanov, E.A., Zvalinsky, V.I., and Leletkin, V.A. 1978. Some mechanisms of light adaptation of coral zooxanthellae. *Dokl. USSR Ac. Sci.* **238:** 1231–1234.

Titlyanov, E.A., Latypov, Y.Y., and Ermak, V.D. 1988a. Effect of light on scleractinian distribution over sublittoral of the Anthoi, Tochu and Condao Islands. In: *Biology of Coral Reefs. Photosynthesis of Reef-Building Corals.* Y.I. Sorokin, ed. Far East Branch USSR Ac. Sci., Vladivostok, pp. 5–18.

Titlyanov, E.A., Kolmakov, P.V., Le Nguen Hieu, Ermak, V.D., Nechay, E.G., Peshehodko, V.M., Lapshina, A.A., and Hoang Thi Lin. 1988b. Structure and production function of coral colonies of *Pocillopora* genus in the light range of their habitat. In: *Biology of Coral Reefs. Photosynthesis of Reef-Building Corals.* Y.I. Sorokin, ed. Far East Branch, USSR Ac. Sci., Vladivostok, pp. 52–71.

Tooming, K.G. and Gulyaev, V.I. 1967. *Methods for Measuring Photosynthetically Active Radiation.* Nauka, Moscow. 143 pp.

Zvalinsky, V.I., Titlyanov, E.A., Leletkin, V.A., and Novozhilov, A.V. 1978. Adaptation of corals to light. In: *Biology of Coral Reefs. Photosynthesis of Zooxanthellae and Macrophytic Algae.* E.V. Krasnov, ed. Far East Science Center, USSR Ac. Sci., Vladivostok, pp. 29–52.