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Acclimation of Symbiotic Reef-Building Corals to Extremely Low Light

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Abstract

This study investigated the photo-acclimation capacity of seven species of hermatypic corals subjected to 2%, 0.8% and 0.1% of incident surface photosynthetic active radiation (PAR_0). *Stylophora pistillata, Porites attenuata* and *Echinopora lamellosa* photoacclimated to 2%, 0.8% and 0.1% PAR_0, *Pocillopora damicornis* only to 2% and 0.8% PAR_0, *Seriatopora caliendrum, S. hystrix* only to 2% PAR_0 and the colonial hydroid *Millepora intricata* could not adapt to light intensity of 2% and lower. Physiological changes associated with photo-acclimation to extremely low light (i.e., 2%, 0.8% and 0.1% PAR_0) were a decline in zooxanthellae population densities, in zooxanthellae sizes, in cell division and degradation. Shade-intolerant species rapidly lost their zooxanthellae in extremely low light treatments and died, whereas shade-tolerant species maintained low zooxanthellae population densities in their tissue during 4 months and more. If the corals *E. lamellosa* and *P. attenuata,* acclimated to extremely low light, were transferred to dim light (30% PAR_0), they regained their initial population densities within 90 days. We assume that specific distinction of corals under acclimation to extremely low light depends mainly on the composition of morphophysiologically and genetically different types of zooxanthellae living in a given colony of certain species.

Keywords: Reef-building corals, photo-acclimation, zooxanthellae, division and degradation of zooxanthellae, chlorophylls

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1. Introduction

The vertical extent and shade-dwelling capacity of hermatypic corals is limited by photosynthetic active radiation. Levels any less than about 1% of incident photosynthetic active radiation (PAR_0) is detrimental, and prolonged exposure to these low levels often leads to coral mortality (Yamazato, 1972; Lang, 1974; Falkowski and Dubinsky, 1981; Fricke and Schuhmacher, 1983; Fricke and Meischner, 1985; Titlyanov and Latypov, 1991). Only *Leptoseris fragilis* is found at lower irradiance levels, for example on deep slopes in the Gulf of Aqaba (Red Sea) (Fricke and Schuhmacher, 1983). However, this species hosts chromatophores that absorb light at short wavelengths and transform the light into longer, more useable, wavelengths (Schlichter et al., 1986, 1988; Schlichter, 1990).

Hermatypic corals generally dwell at depths where the irradiance approximates 80% to 5% PAR_0. In the South China Sea and in the Gulf of Siam about 90% of the coral species were found within this light range (Titlyanov and Latypov, 1991). Some coral species such as *Madracis kirbyi, Montipora hispida, M. aequituberculata, Acropora palifera, A. gemmifera, A. nobilis, Leptoria phrygia* were not found on deep slopes, or in shaded reef habitats, where light intensities were lower than 5% PAR_0 (Titlyanov and Latypov, 1991).

Several authors have shown that most hermatypic corals photoacclimate from 90–70% to 30–10% PAR_0 (Titlyanov et al., 1978, 2000a; Zvalinsky et al., 1978; Falkowski and Dubinsky, 1981; Dustan, 1982; Porter et al., 1984). There appear to be at least three main physiological photo-acclimation mechanisms. First, the corals' capacity to absorb light increases through the accumulation of photosynthetic pigments in the zooxanthellae (Zvalinsky et al., 1978; Titlyanov et al., 1980; Falkowski and Dubinsky, 1981; Porter et al., 1984), through an increase in the thylakoid concentration in chloroplasts (Dubinsky et al., 1984), and/or through an increase in the size of the photosynthetic units (Leletkin et al., 1980; Falkowski and Dubinsky, 1981). Second, the utilization efficiency of absorbed light may increase. Zooxanthellae from shaded colonies have a higher relative quantum yield of photosynthesis than colonies taken from well-lit habitats (Titlyanov et al., 1980; Leletkin, 1988; Zvalinsky, 1988). Third, there may be shifts in the use of photosynthetic products. More intermediate products may be used without their reduction to carbohydrates and lipids (Bil' et al., 1992; Titlyanov et al., 2000a).

Few studies however have assessed the photo-acclimation capacities and survivability of hermatypic corals under extreme low-light treatments (Titlyanov et al., 2000a, 2001a). Usually the maintenance of corals and other cnidarians in low light, or in total darkness, led to bleaching (Franzisket, 1970; Kevin and Hudson, 1979; Müller-Parker, 1984; Sandeman, 1988; Titlyanov et

al., 2001a). Only for *Stylophora pistillata* was it shown that with lowering of light intensity to an extremely low level, do colonies or detached branches survive under these conditions with change in their physiological state: sharp decline in zooxanthellar population density, in pigment concentration (calculated per polyps), at the rate of cell division of symbionts, at the rate of zooxanthellae degradation *in situ* (Titlyanov et al., 2000a, 2001a).

The primary objectives of the present study were to: (1) examine the degree to which hermatypic coral species differ in their tolerances and adaptive capacities under extremely low light; (2) elucidate the mechanisms of photo-acclimation to extremely low light; and (3) determine the possibility of recovery of zooxanthellar population densities following extremely low-light treatments.

2. Materials and Methods

Biological specimens

We collected three medium-sized colonies of the scleractinian corals *Stylophora pistillata* Esper, 1797; *Porites attenuata* Nemenzo 1955; *Echinopora lamellosa* (Esper, 1795); *Pocillopora damicornis* (Linnaeus, 1758); *Seriatopora caliendrum* Ehrenberg, 1834; *S. hystrix* Dana, 1846; and the colonial hydroid *Millepora intricata* Edwards, 1857 (Hydrozoa, Milleporidae) from a fringing reef at Sesoko Island (Okinawa, Japan, (26 38'N, 127 52'E). All colonies were collected from a depth of 1.5–2.5 m of the N–E reef slope (40–20% PAR_0). The colonies were placed in plastic bags and transported to the Tropical Biosphere Research Center, University of Ryukyus. The samples were maintained in a 6-m^3 semi-open, intensively aerated, flow-through aquarium supplied with unfiltered sea water (that had a turnover rate of 30% h^{-1}). A black plastic mesh shaded the aquarium and the light intensity amounted to 30% of incident surface photosynthetic active radiation (PAR_0). The temperature in the aquarium was 25–27°C in the daytime and 23–24°C at night in October 1997; the temperature ranged from 22–24°C in the daytime and 20–22°C at night in February 1998.

Experimental design

The investigations were undertaken from September 1997 to March 1998. Colonies were broken into 4-centimeter pieces (*Echinopora lamellosa)* and 3–5-centimeter exterior branches (*Stylophora pistillata, Seriatopora caliendrum, S. hystrix, Pocillopora damicornis, Porites attenuata, Millepora intricata*), fixed with cement onto ceramic tiles, and replaced in the aquarium. After

reacclimation to the aquarium conditions for 30 days the samples were exposed to different light conditions: that is 2%, 0.8% and 0.1% PAR_0 (at the same aquarium). Incident light was reduced using grey and black plastic mesh. The corals were maintained in the aquarium for 120 days (from October 1997 to February 1998). Coral samples were analyzed twice: after 30 days of pretreatment to dim light (initial variant) and after 120 days of the experiment. In experiments on the study of the dynamics of reacclimation of the corals *E. lamellosa* and *P. attenuata* from 30% to 0.8% and 0.1% PAR_0, respectively, were analyzed on the 5th, 20th, 30th, 40th, 50th, 60th and 120th day. In each treatment (initial and the experiment), three pieces (branches) from three different colonies were analyzed, n = 3.

An additional experiment was undertaken to assess the possible recovery of zooxanthellar population densities when *E. lamellosa* and *P. attenuata* colonies were transferred back to dim light after 90 days of the main experiment. Samples were analyzed on the 5th, 20th, 45th and 90th day of the recovery. In each analysis three coral pieces were used, n = 3.

Analytical procedures

Coral tissue was removed with a Water-Pik (Johannes and Wiebe, 1970) and the number of zooxanthellae in each tissue homogenate sample was counted (10 fields per count) using a hemocytometer. Zooxanthellae density was expressed as number per polyp for *S. pistillata, Seriatopora caliendrum, S. hystrix, P. damicornis, P. attenuata,* or number per cm^2 of coral skeleton surface for *E. lamellosa,* and *M. intricata.* The skeletal surface area was calculated using the aluminium foil technique (Marsh, 1970). The diameter of one hundred (apparently healthy) zooxanthellae were measured from each sample using a calibrated ocular micrometer at ×400 magnification. Zooxanthella volume was calculated using the formula of a sphere.

Proliferating zooxanthellae frequency (PZF) and degrading zooxanthellae frequency (DZF)

Tissue homogenates were observed at 400× on a hemocytometer grid on which we counted normal, dividing and degrading zooxanthellae. Cells in the process of division were classified as such when they showed anything from the initial appearance of a division furrow in the mother cells to the formation of cell envelopes in daughter cells. Degraded or degrading zooxanthellae were identified by color, size and shape after Titlyanov et al. (1996). A total of 500 algae was counted in each sample. The percentage of dividing cells was classified as the proliferating zooxanthellae frequency (PZF), and the

percentage of degrading cells was classified as the degrading zooxanthellae frequency (DZF) in accordance with Titlyanov et al. (1996). PZF and DZF were examined at 9:00–10:00 h, at a time when the number of dividing cells amounts to approximately 80% of the maximum (Titlyanov et al., 1996) and degraded zooxanthellae numbers were highest.

In the scleractinian coral *Echinopora lamellosa* and the hydrocoral *Millepora intricata* DZF indices were not analyzed because a previous experiment showed that there was not a clear daily rhythm in forming and extrusion of zooxanthellar degraded remnants. Part of the remnants can accumulate in polyp tissue and body cavity.

Chlorophyll concentrations

To determine chlorophyll concentrations a known number of zooxanthellae were filtered under a vacuum (47-mm AP Millipore filters) and placed on the filters in a refrigerator for two days in an aqueous solution of 90% acetone. The solution was shaken daily. The absorbance of acetone extracts was measured at 630 and 663 nm using a Hitachi U-2000 spectrophotometer. The concentrations of chlorophyll *a* and chlorophyll c_2 were determined using the spectrophotometric equations of Jeffrey and Humphrey (1975). Chlorophyll concentrations were expressed as μg per mm^3 of the zooxanthellae volume.

Statistical analysis

A Student's *t*-test was used to analyze the data and to evaluate differences between means. Difference between means with $p<0.05$ was considered significant.

3. Results

Habits of branches and fragments of colonies and some polyps after the 120-day experiments are presented in Fig. 1. Not all investigated coral species survived under lowering light intensities from 30% to 2%, 0.8% and 0.1% PAR_0. The hydroid *Millepora intricata* died in 2% PAR_0 (Fig. 1c), *Seriatopora caliendrum* and *S. hystrix* in 0.8% PAR_0 (Figs. 1, 2c) and *Pocillopora damicornis* in 0.1% PAR_0 (Figs. 1f, 2b). The branches of dying corals rapidly lost their zooxanthellae and died having 10–5% of zooxanthellae from initial stock in their tissue. *S. caliendrum* and *S. hystrix* branches survived in 2% PAR_0, *P. damicornis* – in 0.8% PAR_0, *Stylophora pistillata*, *Porites attenuata* and *Echinopora lamellosa* were alive within 120 days of the experiment under light intensities from 2% to 0.1% PAR_0 (Fig. 1).

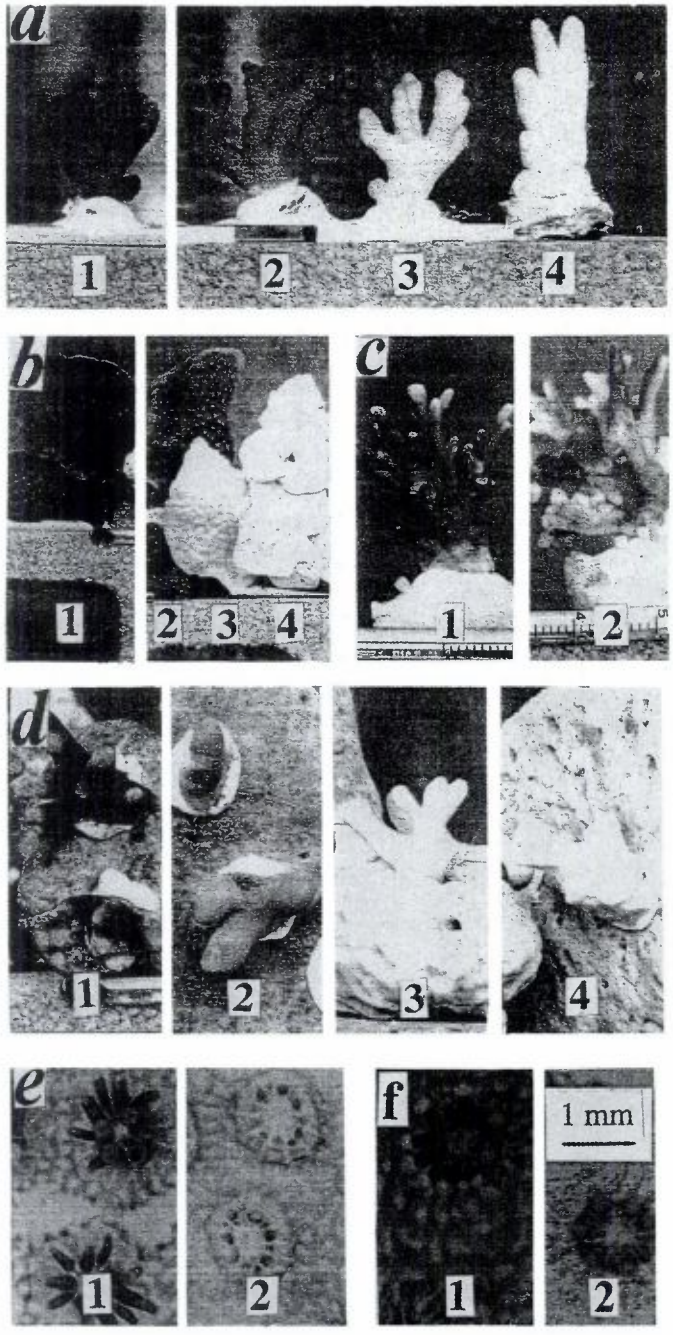

Figure 1. Maintenance of branches and fragments of reef-building corals during 120 days under light intensities: 1) – 30% PAR_0, 2) – 2% PAR_0, 3) – 0.8% PAR_0, and 4) – 0.1% PAR_0: a – *Stylophora pistillata* branches; b – *Echinopora lamellosa* fragments; c – *Millepora intricata* (under 2% PAR_0, dead branch); d – *Porites attenuata* branches; e – *Pocillopora damicornis*, polyps; f – *Seriatopora hystrix* polyps.

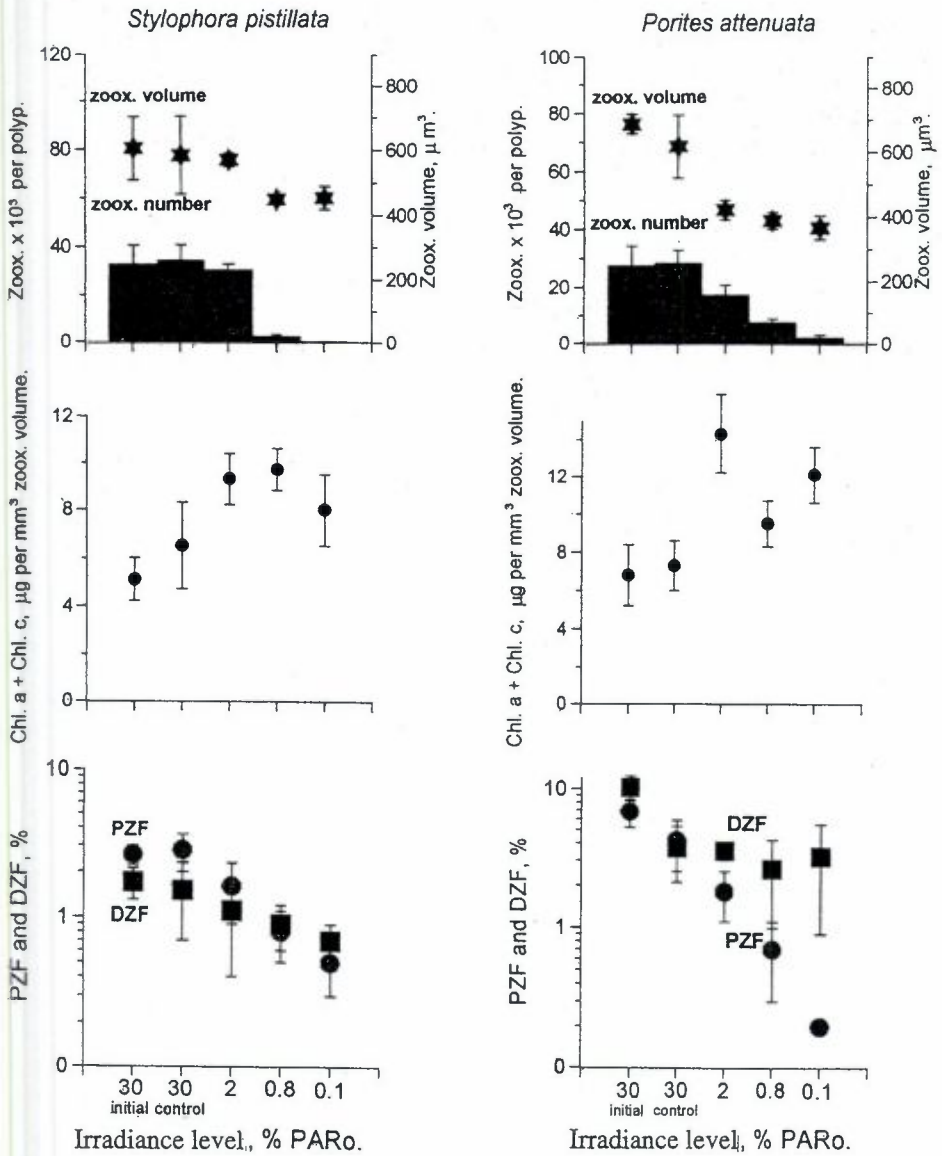

Figure 2a.

Figure 2. Physiological changes in six hermatypic corals subjected to 30% (initial and control), 2%, 0.8% and 0.1% PAR_0: a – *Stylophora pistillata* and *Porites attenuata*; b – *Echinopora lamellosa* and *Pocillopora damicornis*; c – *Seriatopora caliendrum* and *S. hystrix*. Where zoox. number is the zooxanthellae population density; zoox. volume is the zooxanthellae volume; PZF is the proliferating zooxanthellae frequency; and DZF is the degrading zooxanthellae frequency.

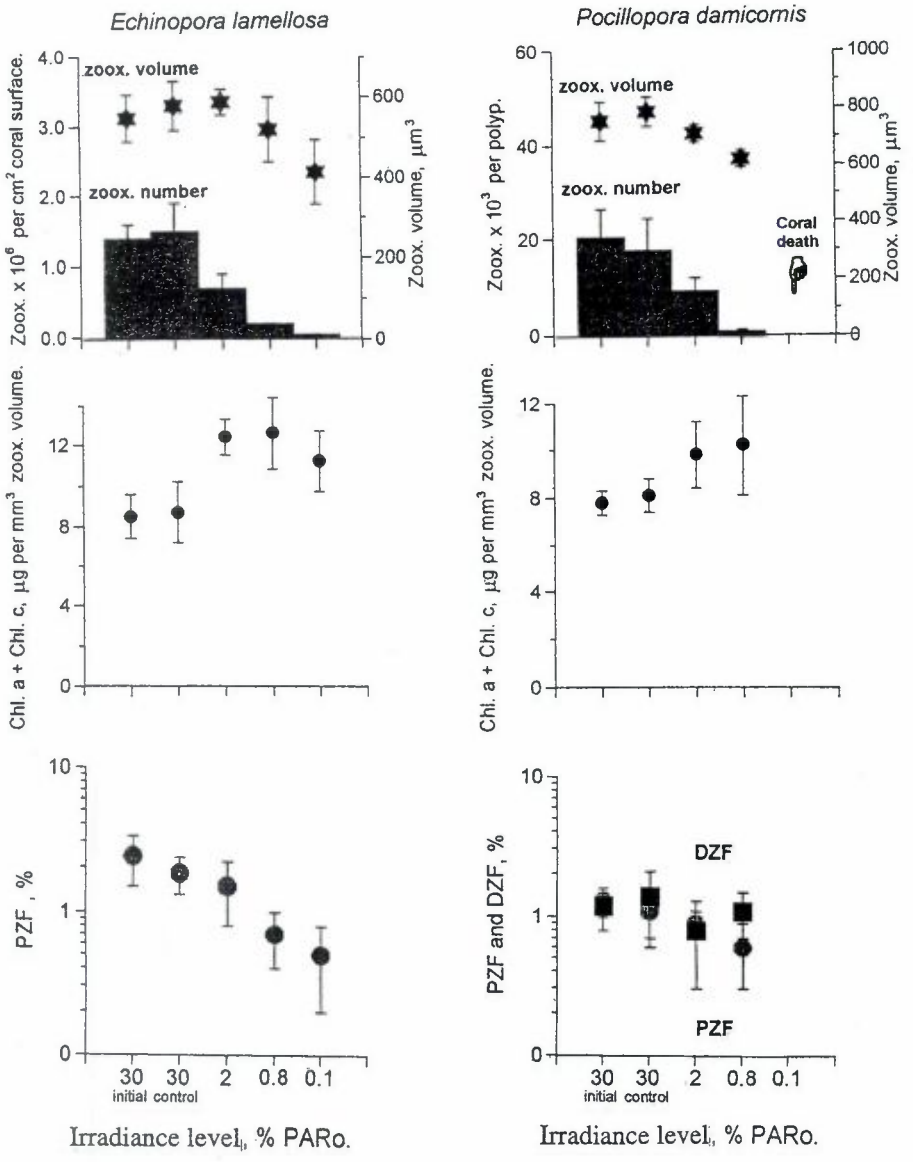

Figure 2b.

All corals survived in extremely low light, responded in the same manner when transferred from 30% to 2% PAR_0 or lower (Fig. 2) by significant reduction in zooxanthellae population density.

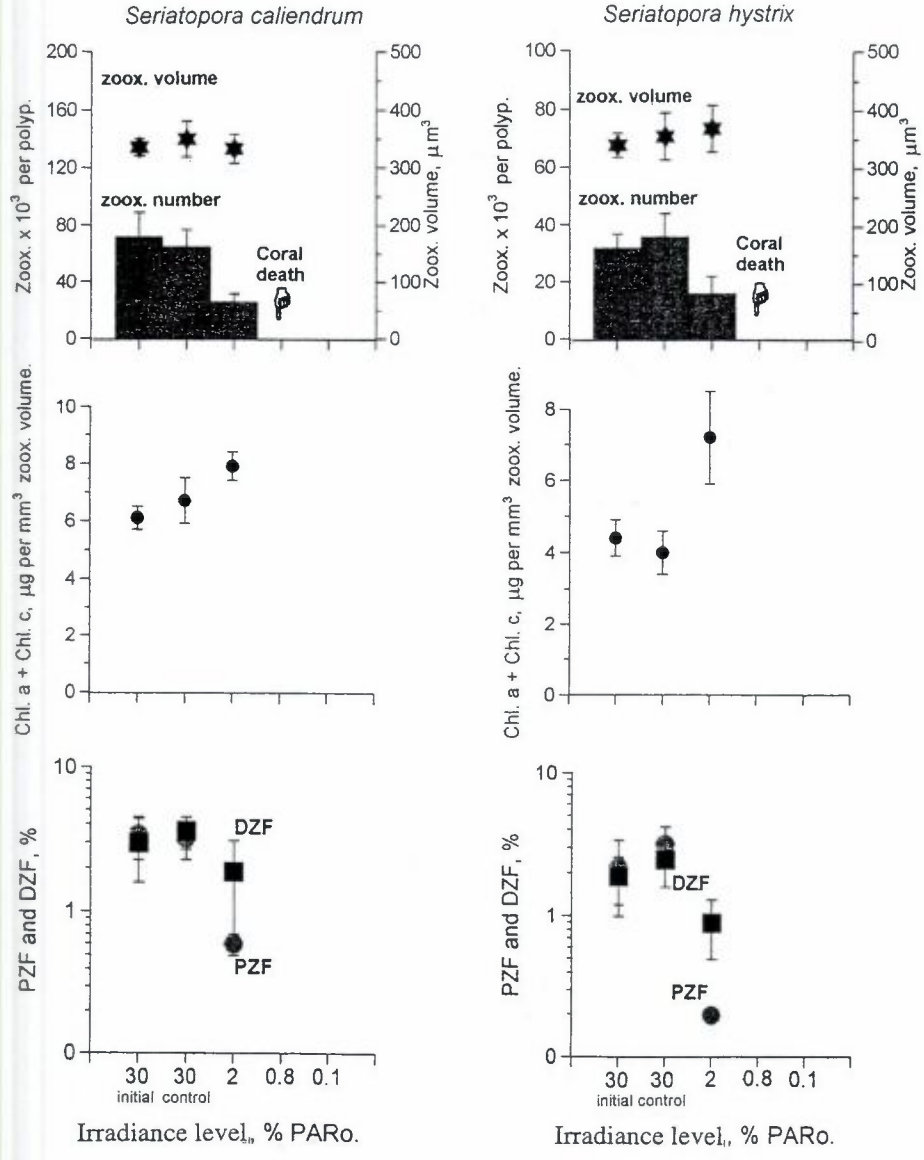

Figure 2c.

Under extremely low light, the zooxanthellae number in *S. caliendrum* and *S. hystrix* (2% PAR_0) dropped 2–2.5-fold, in *P. damicornis* (0.8% PAR_0) – 20-fold, in *S. pistillata*, *P. attenuata* and *E. lamellosa* (0.1% PAR_0) – 20–60-fold.

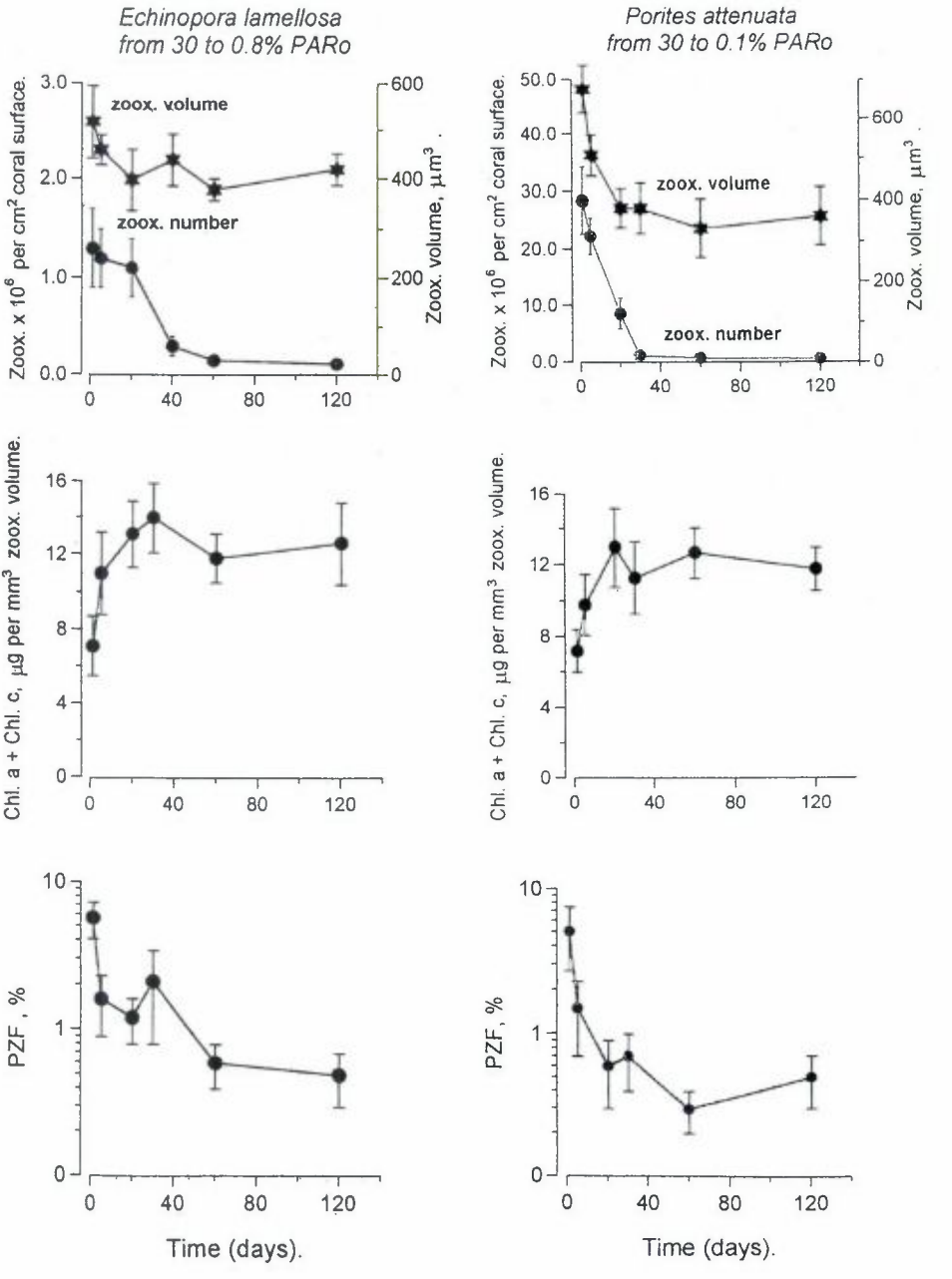

Figure 3a.

Figure 3b.

Figure 3. Physiological changes after transferring the corals *Echinopora lamellosa* from 30% to 0.8% PAR_0 (a) and *Porites attenuata* from 30% to 0.1% PAR_0 (b).

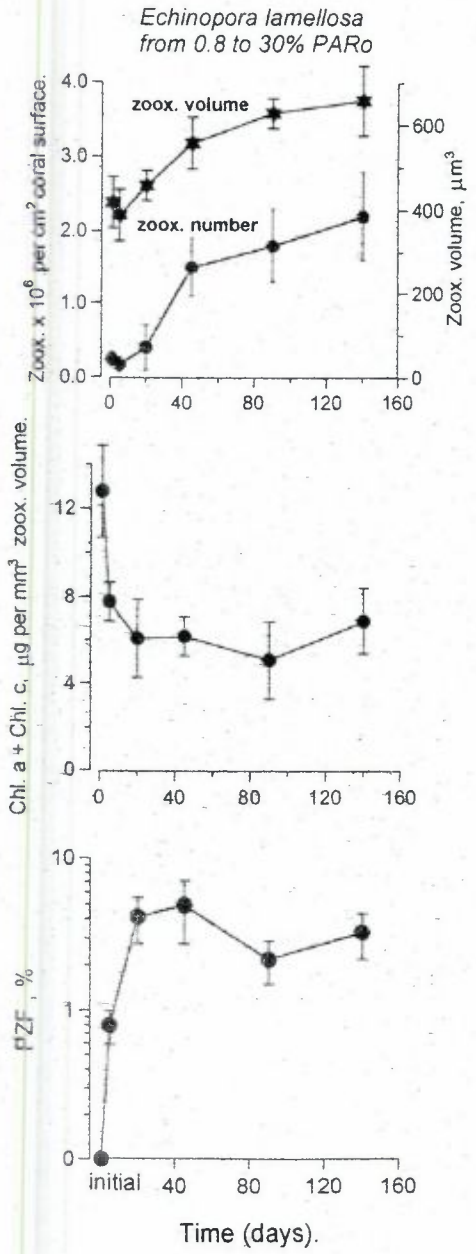

Figure 4a.

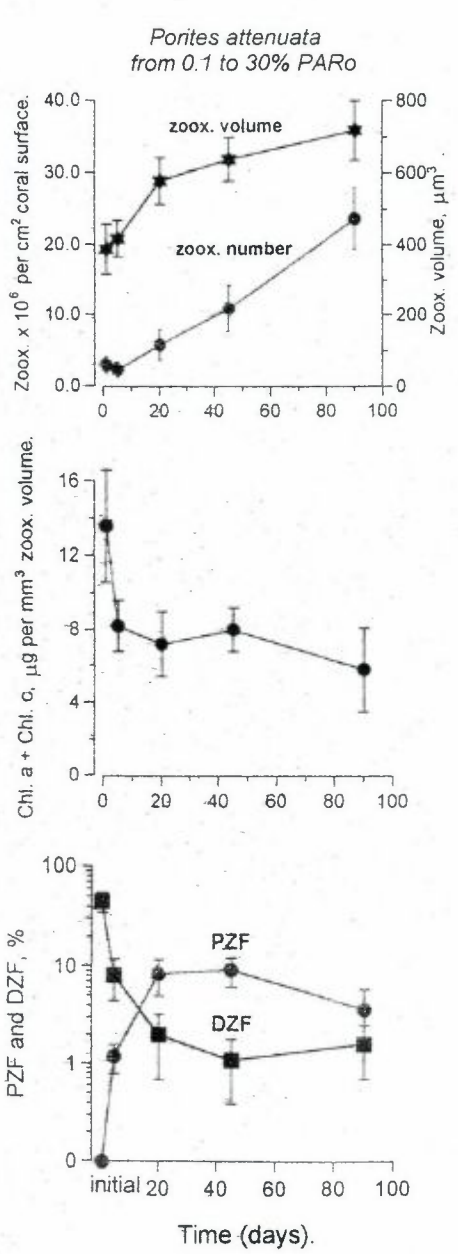

Figure 4b.

Figure 4. Physiological changes after transferring the corals *Echinopora lamellosa* from 0.8% to 30% PAR_0 (a) and *Porites attenuata* from 0.1% to 30% PAR_0 (b).

In all coral species, the PZF level dropped significantly, the DZF level did not change or drop. The ratio PZF to DZF was close to 1.0 (in *P. damicornis* and *S. pistillata)* or was lower than 1.0 in all the rest of the species. The average zooxanthella volume significantly reduced in most coral species (Fig. 2).

Fig. 3 shows the dynamics of main changes in physiological parameters of the corals *E. lamellosa* and *P. attenuata* under reacclimation from 30% to 0.8% and 0.1% PAR_0, respectively. Reduction in zooxanthellae density to minimum numbers occurred approximately within 60 days in both cases. Significant decrease in zooxanthellae sizes occurred during 20 days. Considerable increase (to the average maximum level) in chlorophyll concentration in zooxanthellae, calculated per zooxanthella volume, occurred within the first 5 days of exposure to extremely low light. PZF level dropped to a minimum level during 60 days of the experiment.

Echinopora lamellosa and *Porites attenuata* colonies, subjected to 0.8 and 0.1% PAR_0, and having lost over 90% of their zooxanthellae, recovered their zooxanthellar population densities in 30% PAR_0 (Fig. 4). The zooxanthellar population recovered in *E. lamellosa* within 90 days. The size of the zooxanthellae in *P. attenuata* and *E. lamellosa* significantly increased on the 20th and 45th days of the experiment, respectively. Chlorophyll concentration in zooxanthellae significantly decreased to the 5th day of the experiment in both species. PZF level significantly increased on the 5th day and more than 10-fold within 40 days of the experiment and then changed slightly. DZF level in *P. attenuata* significantly dropped on the 5th day and reached a minimal level on the 20th day. The ratio PZF to DZF was higher than 1.0 within the experiment.

4. Discussion

The majority of the coral species (i.e., *Stylophora pistillata, Porites attenuata, Echinopora lamellosa, Pocillopora damicornis*) displayed a tolerance to extremely low light. The zooxanthellar population densities in these corals decreased substantially, but they remained viable during the four-month experiment. In addition, in such corals as *S. pistillata* and *P. damicornis* the ratio PZF to DZF was about 1 by the end of the experiment. Thus, diel zooxanthellar increase in zooxanthellae number was close to their diel loss that indicates a steady state or complete acclimation to changed light conditions (Titlyanov et al., 1999, 2001a). However, the ratio PZF to DZF in *Seriatopora caliendrum* and *S. hystrix* was lower than 1, which indicated continuation of the acclimation process by reduction in zooxanthellae density and acclimation to extremely low light. Increased DZF level under extremely low light for *P. attenuata,* was probably conditioned by disruption of extrusion

of degraded remnants of zooxanthellae that was shown for *Millepora intricata* and *E. lamellosa* in recent investigations (Titlyanov et al., 2001b). Under 0.1% PAR_0 samples of *P. damicornis* lost all their zooxanthellae within 3–4 months and died. *Seriatopora caliendrum* and *S. hystrix* died under extreme low light (0.8 and 0.1% PAR_0) by 30–60 days of the experiment. The colonial hydroid *M. intricata* was least tolerant to shading; its branches died under 2% PAR_0, 60–90 days of the experiment. Therefore we can devise a hierarchy for our experimental corals in terms of their tolerance to extremely low light: (1) *Stylophora pistillata, Porites attenuata, Echinopora lamellosa,* (2) *Pocillopora damicornis,* (3) *Seriatopora caliendrum, S. hystrix,* and (4) *Millepora intricata* as least tolerant.

In our experiments we measured not only DZF levels which corresponded with extruded remnants of degraded zooxanthellae (Titlyanov et al., 2001a), but expulsion of healthy zooxanthellae also (data are not given). This is evidenced by the expulsion of 10 times less healthy zooxanthellae than the expulsion of degraded zooxanthellae remnants. It was shown that under normal conditions of the experiment the expulsion of healthy zooxanthellae does not play an essential role in zooxanthellae density regulation.

Field data from the South China Sea and from the Gulf of Siam (Titlyanov and Latypov, 1991) showed that *S. pistillata, E. lamellosa* and *P. damicornis* were located in the most shaded sites on the reef, and often at the extremes of vertical distribution where PAR_0 was 2%. Rarely are *M. intricata* and *Seriatopora* species found at great depths on Indo-Pacific reefs (Van Woesik, unpublished data). These field observations concur with our experimental findings.

As was shown by early studies (Dustan, 1982; Porter et al., 1984), the main reactions of acclimation to low light are an increase in photosynthetic pigment concentration in zooxanthellae. Similar acclimation response to low light was found in planktonic microalgae (Dubinsky, 1992), as well as in benthic macroalgae (Talarico and Maranzana, 2000). During the study of acclimation dynamics to light for *S. pistillata* (Titlyanov et al., 2001a) it was shown that significant reduction in light intensity (1.5 times and more) in the habitat caused a signal to accumulation of chlorophylls in zooxanthellae. By reducing the light intensity to approximately 15% PAR_0 or lower – up to 0.1% PAR_0 chlorophylls in zooxanthellae reached maximum concentration (Titlyanov et al., 2000a, 2001a). In our experiment, zooxanthellae of all investigated coral species displayed maximum chlorophyll accumulation when light intensity was reduced from 30% to 2% PAR_0 or lower. We suggest to consider that extremely low light for colonies of certain coral species is a light intensity when the main adaptive reaction to low light by increasing zooxanthellae population density do not display. In our experiment, extremely low light where corals were able to survive for 4 months was the light intensity of 2%

PAR_0 for *Seriatopora caliendrum* and *S. hystrix*, for *Pocillopora damicornis* 0.8% PAR_0, for *Stylophora pistillata*, *Porites attenuata* and *Echinopora lamellosa* – 0.1% PAR_0. Corals were acclimated to extremely low light by increasing chlorophyll concentration in zooxanthellae and decreasing zooxanthellae density in the corals. The same acclimative reactions to extremely low light were found for *S. pistillata* (from the Gulf of Eilat) maintained under 2% PAR_0 with additions of the *Artemia salina* nauplii and from a fringing reef of Sesoko Island under starvation (Titlyanov et al., 2000a).

The experiments on adaptation to extremely low light intensity of the corals *P. attenuata* and *E. lamellosa* (Fig. 3) showed that reduction in zooxanthellae density, in zooxanthellae sizes and in PZF level to constant minimum levels occurred within 40–60 days of the experiment. Chlorophyll concentration in zooxanthellae sharply increased on the 5th day and reached a maximum level on the 10th day of the experiment. In this connection, we assume that even short-term changes in weather conditions (hurricanes, typhoons) with extreme decrease in light intensity in the habitat of corals may lead to changes in the physiological state of the corals: such as decrease in zooxanthellae density and increase in chlorophyll concentration in zooxanthellae.

In the experiment, for the first time, we succeeded in acclimation of scleractinian corals to extremely low light intensity, namely, less than 1% PAR_0. At a later date, after the experiments described in this study, we and other investigators found that corals from the Sesoko fringing reef contained three genetically determined and morphophysiologically different types of zooxanthellae (Titlyanov et al., 2001a, 2001b; Loh et al., 2002; Zhukova, unpublished data). For instance, the hydrocoral *Millepora intricata* contained the largest (13–18 μm in diameter) zooxanthellae of brown color (type L). The zooxanthellae had high chlorophyll concentration (6 to 20 μg chlorophylls per mm^3 of zooxanthellae volume) and the lowest photosynthetic capacities (60–70 μg O_2 per mm^3 of zooxanthellae volume per h). *Pocillopora damicornis* contained zooxanthellae of medium sizes (8–14 μm in diameter) of golden-brown color (type B) and accumulated 4 to 15 μg chlorophylls per mm^3 of zooxanthellae volume. The zooxanthellae had high photosynthetic capacities (70–150 μg O_2 per mm^3 of zooxanthellae volume per h); *Seriatopora caliendrum* and *S. hystrix* contained the smallest zooxanthellae (7–11 μm in diameter) of olive-green color (type G) with the lowest chlorophyll concentration (2 to 8 μg chlorophylls per mm^3 of zooxanthellae volume) and the highest photosynthetic capacities (130–220 μg O_2 per mm^3 of zooxanthellae volume per h). *Stylophora pistillata*, *Echinopora lamellosa* contained a mixture of B and G types of zooxanthellae.

The data presented in this study showed that the corals (*Pocillopora damicornis*, *S. pistillata*, *E. lamellosa*, *Porites attenuata*), containing

zooxanthellae of the type B, are most shade-tolerant in comparison with the coral *Millepora intricata* containing zooxanthellae of type L and with the *Seriatopora* species containing zooxanthellae of type G. It is a basis to assume that tolerance of corals to extremely low light intensities depend on composition of symbionts in coral tissue. As was shown in previous investigations on reacclimation from 95% to 30–8% PAR_0 of some scleractinian coral species containing both types (B and G) of zooxanthellae, the corals accumulated relatively more of zooxanthellae of type B. Under reacclimation to bright light corals accumulated zooxanthellae of type G.

Existence of the mixture of different taxa of zooxanthellae (clades A, B, C) in coral species from Caribbean was shown for the first time by Rowan and Powers in 1991. Then it was shown by many authors for corals from different areas of the World Ocean (e.g., Aisyah et al., 2000; Belda-Baillie et al., 2000; Diekmann et al., 2000; Hidaka and Hirose, 2000; Loh et al., 2000; Rodriguez-Lanetty et al., 2000; Savage and Douglas, 2000). The possibility to form a certain composition of populations of genetically determined zooxanthellae in the coral *Montastrea annularis* and *M. faveolata* in dependence upon the shade in the habitat was shown in previous studies by Rowan and Knowlton (1995) and by Rowan et al. (1997). Avon et al. (2000) showed for the coral *Acropora palifera* from Taiwan that seasonal variation type composition of symbiont community may occur in some colonies. At the same time, as it was shown for *Acropora digitifera* from Akajima reef, Japan (Belda-Baillie et al., 2000) the mixed algal populations showed general consistency over the different seasons.

Adaptation of corals to extremely low light led not only to the reduction in zooxanthellae population density, decrease in zooxanthellae sizes and decline in the levels of zooxanthellae division and degradation (Fig. 2), but also to a decline in dark respiration both in the coral (Wethey and Porter, 1976; Falkowski and Dubinsky, 1981) and in the symbionts (Zvalinsky et al., 1980; Leletkin et al., 1996); a reduction in the level of excretion (Crossland, 1987); and a shift of the photosynthetic assimilation of carbon into glycerol, rather than into hexoses (Bil' et al., 1992; Titlyanov et al., 2000a). These changes give a basis to consider that under acclimation of corals to extremely low light intensity, they change to new significantly lower levels of metabolism which is provided by energy and substances mainly by heterotrophic consumption of organic remnants and dissolved organic matter (DOM) and partially by digestion of their own zooxanthellae (Sorokin, 1990; Titlyanov et al., 1996, 2000c).

Shade-tolerant corals that lost more than 90% of zooxanthellae under acclimation to extremely low light, were capable of accumulating zooxanthellae after transfer to dim light (30% PAR_0). Complete recovery of zooxanthellae density and the level of metabolism occurred after 3–4 months of maintenance under dim light. During the recovery it was found that the

zooxanthellae increased in size, and chlorophyll concentration decreased. The PZF level was considerably higher than the DZF level which confirms our assumption that under normal physiological conditions an increase and decline in symbiont density of corals is regulated by the rates of two processes: by division and degradation of zooxanthellae (Titlyanov et al., 2000b).

Reduction in zooxanthellae density under extremely low light and recovery of the density with increasing light intensity allows us to suppose that coral bleaching under extremely low light may be a normal physiological process providing a vital function of corals under these extreme conditions and giving the possibility to again accumulate an essential number of zooxanthellae (with rising autotrophic production of corals) after increase of the light intensity.

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