

Photoinhibition in shallow-water colonies of the coral *Stylophora pistillata* as measured in situ

Gidon Winters

Department of Plant Sciences, Tel Aviv University, Tel Aviv 69978, Israel

Yossi Loya

Department of Zoology, Tel Aviv University, Tel Aviv 69978, Israel

Rüdiger Röttgers

GKSS Research Center Geesthacht, Institute for Coastal Research, Biooptical Remote Sensing, Max-Planck-Str., D-21502 Geesthacht, Germany

Sven Beer¹

Department of Plant Sciences, Tel Aviv University, Tel Aviv 69978, Israel

Abstract

Continuous pulse amplitude–modulated (PAM) fluorescence measurements were performed in situ under natural irradiances for colonies of the coral *Stylophora pistillata* growing in shallow (2 m) and deeper (11 m) waters of the Red Sea. The effective quantum yield ($\Delta F/F'_m$) showed a diurnal pattern inversely related to that of the incident downwelling photosynthetically available radiation (PAR), but this pattern was skewed for the shallow colonies such that the values were always lower in the afternoon than during morning hours when measured at similar irradiances. Accordingly, the relative photosynthetic electron transport rate (rETR, = $\Delta F/F'_m \times$ incident PAR) for those colonies also showed lower values in the afternoons than in the mornings at equal irradiances. The rETRs also saturated well before maximal midday irradiances occurred. At the same time, nonphotochemical quenching (NPQ, measured as $[F_m - F'_m]/F'_m$) was higher in the afternoons than during the mornings under similar incident PAR values. These results indicate an afternoon loss in photosynthetic capacity from photoinhibition. Such photoinhibition was not apparent during the course of the day in the corals growing in deeper water. The latter also showed no saturation of photosynthesis at the highest incident PAR values at noon (which were approximately a third of those at the shallower site). In addition, the shallow-growing corals showed significantly lower maximum quantum yields ($\Delta F/F'_m$ measured during nighttime, equivalent to F_v/F_m) than the deeper growing ones. This is most likely caused by an additional, more chronic, photoinhibition in the shallow-growing corals but could also be due to some form of photoacclimation or to factors other than light.

Photoinhibition has been defined as reduced photosynthetic efficiency (quantum yield, Henley et al. 1991; Franklin and Foster 1997) or capacity (photosynthetic rate, Kok 1956; Kirk 1994), or both, at excess irradiance. Until at least a decade ago, such photoinhibition had not been reported for corals, and the existence of this phenomenon in the coral reef environment was questionable (Muscatine 1980; Dubinsky et al. 1990; Falkowski et al. 1990; Franklin et al. 1996).

With the continuing improvements of nonintrusive techniques for measuring quantum yields, photoinhibition has recently been reported to occur in some corals. Measuring chlorophyll fluorescence of in hospite zooxanthellae with an underwater pulse amplitude–modulated (PAM) fluorometer, Brown et al. (1999) and Hoegh-Guldberg and Jones (1999) reported on dynamic photoinhibition based on midday depressions of maximum quantum yields (F_v/F_m , measured after periods of dark adaptation). However, both those studies were performed on corals held in aquariums, albeit under sunlight conditions, and such confinements could have imposed stressful changes in the organisms and complicated

extrapolations of the results to natural, in situ, conditions. With the development of the Diving-PAM, measurements of chlorophyll fluorescence became applicable also for in situ research of coral photosynthesis (Beer et al. 1998; Ralph et al. 1999). However, those in situ works did not make use of the ambient irradiance during the measurements. Rather, the Diving-PAM's internal halogen light source was used to irradiate the corals, thus generating so-called "rapid light curves." Using submersible fluorometers, it is also possible to perform photosynthetic measurements of corals in situ under ambient irradiances. The only measurements performed so far under such conditions were done with a fast repetition rate (FRR) fluorometer (Gorbunov et al. 2001; Lesser and Gorbunov 2001). They showed midday depressions of $\Delta F/F'_m$ for several Caribbean species, and Gorbunov et al. (2001) concluded most of this to be due to dynamic photoinhibition. However, neither of these studies, nor the ones by Brown et al. (1999) and Hoegh-Guldberg and Jones (1999), showed loss of photochemical capacity, which would fit the more classic definition of photoinhibition (e.g., Kirk 1994).

In this work, we describe diel changes in $\Delta F/F'_m$ and the

¹ Corresponding author (svenbeer@post.tau.ac.il).

relative electron transport rate (rETR) of zooxanthellae residing within shallow and deeper growing colonies of *Stylophora pistillata* as measured in situ under natural irradiances. In shallow-growing colonies, photoinhibition was expressed both as decreased rETRs and concomitantly increased values of nonphotochemical quenching (NPQ) in the afternoons relative to the morning hours, when compared under similar incident photosynthetically available radiation (PAR) values. In addition, the shallow colonies showed lower F_v/F_m values than those measured for the deeper growing ones.

Materials and methods

Measurements were carried out during September and October 2000 on colonies of *S. pistillata*, a dominant coral species of the Red Sea. The colonies investigated grew at water depths of 2 and 11 m in front of the Inter University Institute (IUI) located on the northwestern shore of the Gulf of Aqaba (Red Sea), just south of Eilat, Israel (29°30'N, 34°55'E). The water temperature during the measurement period was $25.5 \pm 1.0^\circ\text{C}$. All fluorescence measurements were performed in situ using an underwater PAM fluorometer (Diving-PAM, Walz). Several 24-h measurement series were done for both shallow ($n = 10$) and deep ($n = 8$) colonies at their horizontal tips. The Diving-PAM itself was placed in a plastic basket secured to the bottom, and a specially built flexible holder attached to a tripod held its optical fiber in place ~ 1 cm from the coral surface. These measurements were always made in such a way that the measured (top-facing) section of the coral branch never became shaded during the course of the day. In situ downwelling photosynthetically active (400–700 nm) radiation (PAR_L) was measured at 1-min intervals using an underwater quantum sensor (LI-192SA, Li-Cor, hence the subscript L in PAR_L) located about 50 cm beside the corals and connected to a Datalogger (LI-1000, Li-Cor). In addition, the downwelling irradiance closer to the particular coral being investigated was measured by the Diving-PAM's quantum sensor (hence, PAR_D), which had been calibrated against a LI-189 quantum sensor (Li-Cor). This sensor was placed horizontally on the flexible holder, close to the tip of the Diving-PAM's optical fiber. Measurements of fluorescence parameters and PAR_D were done automatically every 30 min over 24-h periods as set by the Diving-PAM's internal timer. The water temperature was recorded by the Diving-PAM's internal thermometer.

The effective quantum yield of photosystem II (PSII) ($\Delta F/F'_m$) was measured as $(F'_m - F)/F'_m (= \Delta F/F'_m)$ (Genty et al. 1989; Schreiber et al. 1994), where F is the fluorescence yield under ambient light (steady state fluorescence) and F'_m is the maximum fluorescence yield sampled after a 0.8-s period of saturating light ($\sim 10,000 \mu\text{mol photons m}^{-2} \text{s}^{-1}$). The effective quantum yield as measured during nighttime is actually equivalent to the maximum quantum yield, frequently termed F_v/F_m , where F_m is the maximum fluorescence yield in a dark-adapted plant following a short period of saturating light and F_v is the variable fluorescence ($F_v = F_m - F_0$; F_0 is the minimum steady state fluorescence yield measured in close-to-darkness). rETRs were calculated as

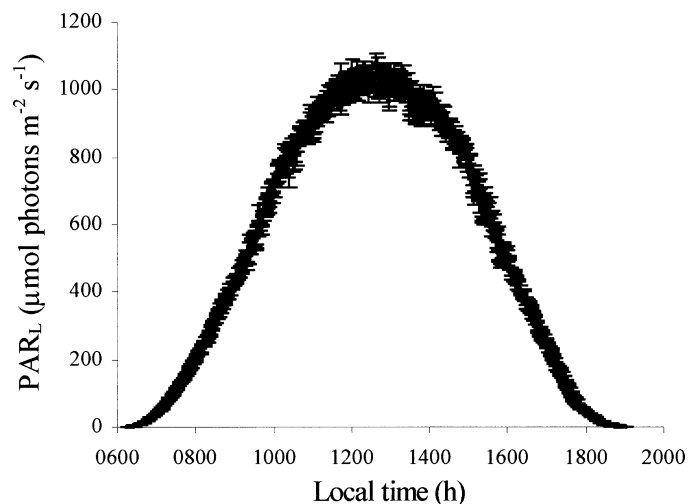


Fig. 1. Average diurnal cycle (\pm SE) of downwelling photosynthetically active radiation (PAR_L), measured at 2 m water depth using a Li-Cor underwater quantum sensor, for 15 d within the period 16 September–4 October 2000. The PAR_L values were recorded every minute.

$\Delta F/F'_m \times \text{PAR}_D$. The rETR values given here are relative because we did not consider the fraction of light absorbed by the photosynthetic pigments of the zooxanthellae within the coral tissue (see also Hoegh-Guldberg and Jones 1999) or the distribution of absorbed light between pigments associated with the two photosystems.

NPQ was calculated as $(F_m - F'_m)/F'_m$ (cf. Hoegh-Guldberg and Jones 1999). The F_m values used were taken from the highest value measured during the night.

Results

The average downwelling PAR_L irradiance measured at a depth of 2 m for 15 d during late September to early October 2000 is presented in Fig. 1. Short-term fluctuations within each day were due to wave movements during the measurements, and the slight variations between consecutive days represent differences in water turbidity. The high midday irradiances at this depth reflect the clear waters of the Red Sea in combination with the typically very bright, cloudless days.

A high correlation ($r = 0.951$, slope = 1.037) was found between the irradiances measured using the Li-Cor underwater quantum sensor (PAR_L) and those measured with the Diving-PAM's quantum sensor (PAR_D). Hence, for calculations of rETRs, we used values of PAR_D (which were recorded closer to the actual coral branches for which also the fluorescence parameters were measured).

An example of in situ measured diel changes in PAR_D , F , F'_m , and $\Delta F/F'_m$ for a shallow-growing (2 m depth) *S. pistillata* colony is shown in Fig. 2. Diurnal patterns of both F and F'_m approximately mirrored that of PAR_D and were further characterized by a peak at dawn, followed by a decrease during the morning and a minimum at midday. An approximately reciprocal increase was found in the afternoon, followed by a peak at dusk. Diurnal patterns of $\Delta F/F'_m$ also

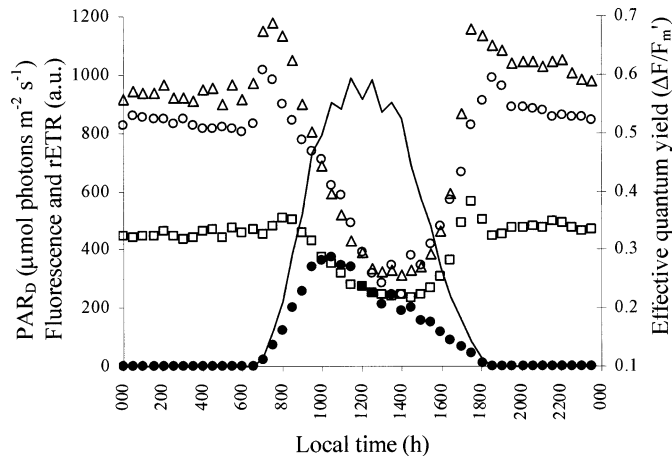


Fig. 2. An example of the diel pattern of downwelling photosynthetically active radiation (PAR_D , continuous line), minimal (F_m , squares) and maximal (F'_m , triangles) fluorescence, effective quantum yield ($\Delta F/F'_m$, unfilled circles), and relative electron transport rate (rETR, filled circles) measured for *Stylophora pistillata* growing at 2 m depth. All measurements were made on 29 September 2000 at intervals of 30 min.

approximately mirrored the changes in PAR_D . $\Delta F/F'_m$ values were 0.51–0.53 during the night. Starting from sunrise, rETRs increased with increasing PAR_D . The rETR was in this example saturated by 0945 h (at $\sim 700 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$), although maximum PAR_D ($\sim 980 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$) was not reached until more than 2 h later. rETR stayed at this saturated level for 2–3 h, after which it started to decline, although irradiance levels started to decrease only 2.5 h later.

The same rETR data as in Fig. 2 was also plotted as a function of PAR_D , resulting in the bold rETR versus PAR_D (i.e., photosynthesis vs. irradiance) curve of Fig. 3. This curve demonstrates the overall nonlinear relationship between rETR and PAR, with saturation of rETR beginning in this example at around $700 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$. In this, as in all other colonies measured at 2 m depth (three of which are also depicted in Fig. 3), the rETRs obtained during the morning hours (represented by the upper parts of the “looping” curves) show higher values than those measured during the afternoon (the lower part of the curves) at comparable irradiances. Plotting NPQ as a function of PAR_D (Fig. 4) yielded an opposite trend from that of the rETR versus irradiance plots (i.e., NPQ was higher in the afternoon than during the morning when compared under the same irradiances). The hysteresis in the rETR versus PAR_D curves of Fig. 3, caused by loss of photosynthetic activity during the afternoon, indicates the presence of photoinhibition, which is further evidenced by the reciprocally higher levels of NPQ during the afternoons. The possible damage caused by this photoinhibition is apparently repaired within the late afternoon, as exemplified by the similar F_m , F'_m , and $\Delta F/F'_m$ values measured after dusk and just before the following dawn (Fig. 2).

In the example for colonies of *S. pistillata* measured at 11 m (Fig. 5), the maximal PAR_D reached $390 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$, which is about a third of that measured for the

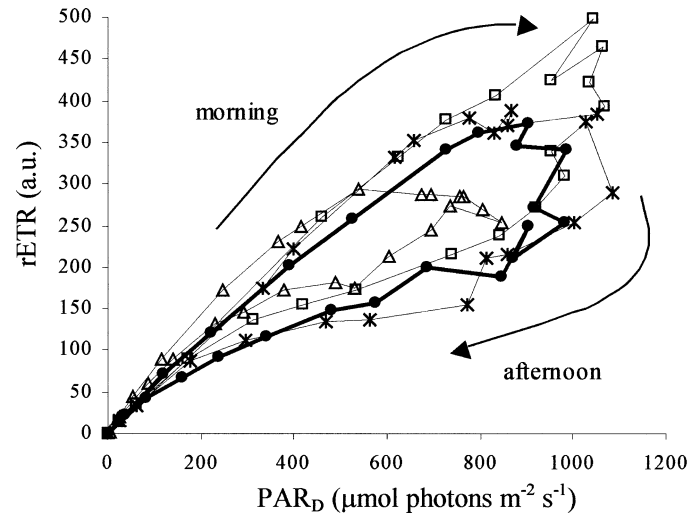


Fig. 3. Relative electron transport rates (rETR) measured for *Stylophora pistillata* growing at a depth of 2 m as a function of downwelling photosynthetically active radiation (PAR_D) measured at the same time and depth using the Diving-PAM's quantum sensor. The measurements are divided into morning (\rightarrow) and afternoon (\leftarrow) values. Measurements were done on 10 (triangles), 15 (squares), 17 (unfilled circles), and 29 (filled circles) September 2000.

colonies at 2 m. The general diurnal pattern of $\Delta F/F'_m$ measured for this deeper growing coral was similar to those of the shallow-growing colonies. However, the 8% midday drop in $\Delta F/F'_m$ (down to 0.58 in this example) was minute compared to that experienced by the shallow-growing coral (a 63% midday drop in the example shown in Fig. 2). Unlike the findings for the shallow corals, the diel pattern of rETR in the deeper corals followed very closely that of PAR_D : midday maximal rETR was reached at the same time as max-

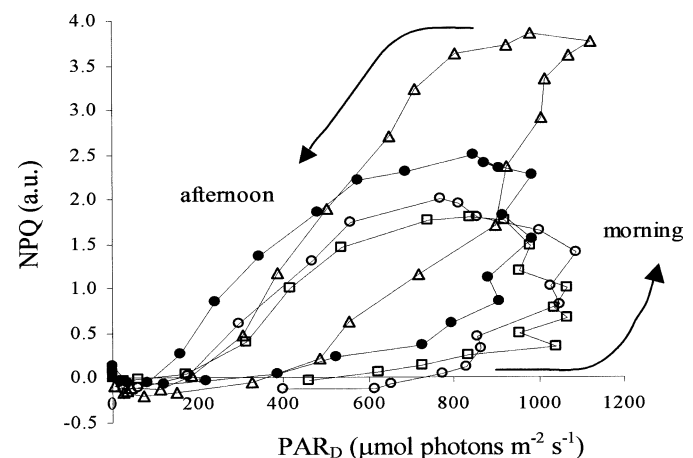


Fig. 4. Nonphotochemical quenching (NPQ) measured for *Stylophora pistillata* growing at a depth of 2 m as a function of downwelling photosynthetically active radiation (PAR_D). NPQ was calculated as $(F_m - F'_m)/F'_m$; the F_m values were taken from the highest one measured during the night. The measurements are divided into morning (\rightarrow) and afternoon (\leftarrow) values. Measurements were done on 10 (triangles), 15 (squares), 17 (unfilled circles), and 29 (filled circles) September 2000.

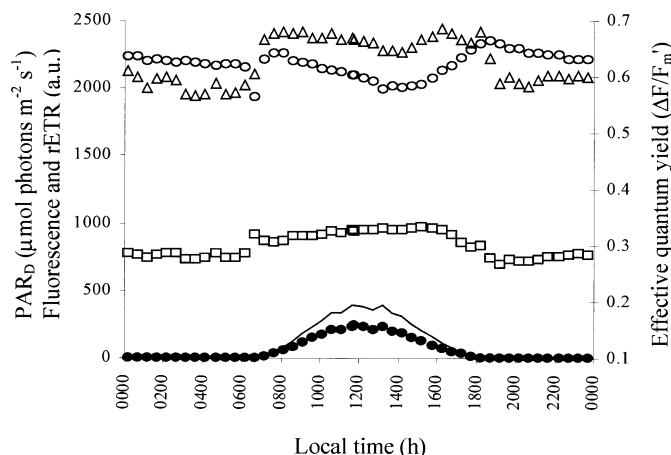


Fig. 5. An example of the diel pattern of downwelling photosynthetically active radiation (PAR_D , continuous line), minimal (F , squares) and maximal (F'_m , triangles) fluorescence, effective quantum yield ($\Delta F/F'_m$, unfilled circles), and relative electron transport rate (rETR, filled circles) measured for *Stylophora pistillata* growing at 11 m depth. All measurements were made on 5 October 2000 at intervals of 30 min. Note the different left y-axis scale compared with Fig. 2.

imal PAR_D , the afternoon decline in rETR started with the decline in afternoon irradiances, and no daily pattern of photoinhibition was found. The nighttime maximum effective quantum yield (equivalent to F_v/F_m) measured for the deeper coral was also some 20% higher than that measured for their shallow counterparts. This indicates that the latter also experienced some type of more persistent photoinhibition as compared with the deeper growing forms.

The same rETR data as in Fig. 5 were also plotted as a function of PAR_D , resulting in the bold rETR versus PAR_D curve of Fig. 6. In this example, as in another one shown in the same figure, saturation of rETR was not reached, and the rETRs measured during the morning hours were very similar to those measured during the afternoon at comparable irradiances. The same principal pattern was found for all colonies growing at 11 m depth. Therefore, the loss of photosynthetic activity during the afternoon, which was found to occur in shallow corals, does not take place in the deeper growing colonies. Nonphotochemical quenching analysis performed for the deep colonies did not show any logical patterns of variation from before to after noon (data not shown).

Discussion

The general daily patterns of $\Delta F/F'_m$ described in this study for *S. pistillata* are similar to the patterns of F_v/F_m shown for zooxanthellae of *Goniastrea aspera* (Brown et al. 1999) and *S. pistillata* and *Porites cylindrica* (Hoegh-Guldberg and Jones 1999). Although photosynthetic rates were not measured, the midday decreases in F_v/F_m in the latter studies were conceived as dynamic photoinhibition. In addition, those studies were not performed in situ, but on corals held in aquariums, which might have been further stressed by the methods of dark adaptation used prior to the mea-

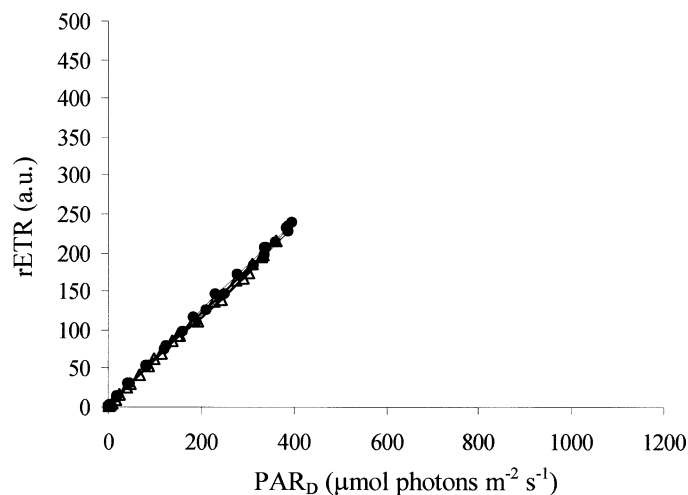


Fig. 6. Relative electron transport rates (rETR) measured for *Stylophora pistillata* growing at a depth of 11 m as a function of downwelling photosynthetically active radiation (PAR_D) measured at the same time and depth using the Diving-PAM's quantum sensor. The measurements were done on 5 (circles) and 8 (triangles) October 2000.

surements. Using the last data point of rapid light curves performed in situ for several species at different times of the day, Ralph et al. (1999) found similar midday depressions in maximum ETR and explained this also to be dynamic photoinhibition. In contrast to the above studies, the measurements in our study were performed in situ and under natural irradiances (without dark adaptations). In this work, the conclusion of photoinhibition in shallow-growing colonies of *S. pistillata* is based on the hysteresis of the daily rETR versus PAR_D (photosynthesis vs. natural daily irradiance) curves, as well as on the converse hysteresis of NPQ.

The only other continuous nonintrusive in situ diel measurements of $\Delta F/F'_m$ and ETR reported for corals under natural irradiances were performed on shallow-growing (2 m depth) *Montastraea faveolata* in the Caribbean using a fast repetition rate (FRR) fluorometer (Gorbunov et al. 2001). The diel patterns found in our study for the shallow-growing *S. pistillata* are similar to those of that study, with the exception of two findings. First, nighttime (maximum) values of the quantum yields measured in the latter study were lower (~ 0.4) compared to those we measured for *S. pistillata* growing at 2 m near Eilat (~ 0.55 – 0.60). Although the variation between the two studies could be attributed to different temperatures, seasons, and species, it is most likely due to the different types of fluorometers used; the FRR measurements are based on single turnovers of PSII (Kolber et al. 1998), whereas PAM measurements are based on multiple turnovers (Samson et al. 1999.) This is supported by the relatively low nighttime $\Delta F/F'_m$ values (~ 0.45) recently measured for *Favia fava* in Eilat using such an FRR fluorometer (Oren Levy pers. comm.) as compared to PAM fluorometer values (~ 0.6 , Gidon Winters, unpubl. data).

The second principal difference between our results and those of Gorbunov et al. (2001) lies in the fluorescence data during dawn and dusk. Unlike our study, in which F , F'_m , and $\Delta F/F'_m$ showed an increase during dawn and dusk, Gor-

bunov et al. (2001) found that F'_m and $\Delta F/F'_m$ (but not F) actually decreased during dawn but remained without a marked change during dusk. They explained the early morning decreases in F'_m and $\Delta F/F'_m$ as a time lag in the activation of the Calvin cycle. The phenomenon of dawn and dusk "peaks" in various fluorescence parameters, as demonstrated in our study, has also been shown before in macroalgae (Henley et al. 1991; Hanelt et al. 1993), as well as in the corals *Acropora aspera*, *Goniastrea* sp., and *Porites* sp. (Ralph et al. 1999) and in *P. cylindrica* and *S. pistillata* (Hoegh-Guldberg and Jones 1999). Although the latter offered no explanation for the rapid dawn and dusk increases in F_v/F_m , they did explain similar findings for *Montipora digitata* and *S. pistillata* in a later study as being evidence of state transitions (Jones and Hoegh-Guldberg 2001).

A comparison of *S. pistillata* growing at 2 and 11 m resulted in two main findings. First, we found that photoinhibition, as indicated by the loss of photosynthetic capacity during the afternoon, did not occur in the deeper corals. This is not surprising since, judging from the rETR versus PAR_D curves, the deeper colonies were never even light saturated during the course of the day (whereas light saturation was found to occur in the shallow-growing ones). Lack of such photoinhibition in the deeper colonies could thus be due to the approximately three times lower PAR measured at 11 m compared with colonies at 2 m or possibly to the lower UV radiation at such depths (UV radiation was not measured here; however, see Gleason and Wellington [1993] for a similar conclusion) or to both. Second, we found the maximum quantum yields (measured at nighttime) for deeper colonies to be significantly higher than those of the shallower ones, indicating the possibility of a longer-term "chronic" photoinhibition in the shallower corals caused by the constant daytime exposure to high doses of visible and UV radiation. Similar results were also obtained by Wyman et al. (1987) and Lesser and Gorbunov (2001). Similar indications for chronic photoinhibition were also reported by Gorbunov et al. (2001), who found higher nighttime $\Delta F/F'_m$ (i.e., F_v/F_m) in corals growing in the shade, compared to their counterparts at the same depth growing unshaded. A further way to interpret higher nighttime $\Delta F/F'_m$ values for deeper (low-light) corals in comparison with shallower water (high-light) colonies could be photoacclimatization of the deeper colonies to their relatively low light environment. This is supported by the many studies on changes that occur in the cellular concentration of photosynthetic pigments (Falkowski and Dubinsky 1981; Dubinsky et al. 1984; Iglesias-Prieto and Trench 1994), productivity, and the optical properties of corals with depth (Dunstan 1982; Dubinsky et al. 1984; Wyman et al. 1987) but could also be due to differences in factors other than light.

Because of the arid climate around the Gulf of Aqaba, corals growing in its shallow waters are exposed to higher annual PAR doses than in most other tropical areas. Multi-year meteorological surveys report a mean incident insolation of $>230 \text{ W m}^{-2} \text{ d}^{-1}$ (based on data collected during 1990–1998 from the meteorological station in Eilat, located 12 m above the sea surface; Sokoletsky et al. in press) with an annual mean of cloudiness that is $<15\%$ (Atlas of Israel 1985). The zooxanthellae residing within corals growing in

shallow waters of the Red Sea area could therefore be expected to have acclimatized to such high irradiances by photosynthesizing according to their maximum capacity at all times. However, the hysteresis in the rETR versus PAR_D (i.e., photosynthesis vs. natural incident irradiance) curves found for shallow-growing *S. pistillata* clearly demonstrates that this is not the case.

References

- ATLAS OF ISRAEL. 1985. Survey of Israel, 3rd Ed. Ministry of Housing. Carta, Jerusalem.
- BEER, S., M. ILAN, A. ESHEL, A. WEIL, AND I. BRICKNER. 1998. The use of pulse amplitude for in situ measurements of photosynthesis in two Red Sea faviid corals. *Mar. Biol.* **131**: 607–612.
- BROWN, B. E., I. AMBARSARI, M. E. WARNER, W. K. FITT, R. P. DUNNE, S. W. GIBB, AND D. G. CUMMINGS. 1999. Diurnal changes in photochemical efficiency and xanthophyll concentrations in shallow water reef corals: Evidence for photoinhibition and photoprotection. *Coral Reefs* **18**: 99–105.
- DUBINSKY, Z., P. G. FALKOWSKI, J. W. PORTER, AND L. MUSCATINE. 1984. Absorption and utilization of radiant energy by light and shade adapted colonies of hermatypic coral *Stylophora pistillata*. *Proc. R. Soc. Lond. B.* **222**: 203–214.
- , N. STAMBLER, M. BEN ZION, L. R. MCCLOSKEY, L. MUSCATINE, AND P. G. FALKOWSKI. 1990. The effect of external nutrient resources on the optical properties and photosynthetic efficiency of *Stylophora pistillata*. *Proc. R. Soc. Lond. B.* **239**: 231–246.
- DUNSTAN, P. 1982. Depth-dependent photoadaptation by zooxanthellae of the reef coral *Montastraea annularis*. *Mar. Biol.* **68**: 253–264.
- FALKOWSKI, P. G., AND Z. DUBINSKY. 1981. Light–shade adaptation of *Stylophora pistillata*, a hermatypic coral from the Gulf of Eilat. *Nature* **289**: 172–174.
- , P. L. JOKIEL, AND R. A. KINZIE III. 1990. Irradiance and corals, p. 89–107. In Z. Dubinsky [ed.], *Ecosystems of the world: Coral reefs*. Elsevier.
- FRANKLIN, L. A., AND R. M. FOSTER. 1997. The changing irradiance environment: Consequences for marine macrophyte physiology, productivity and ecology. *Eur. J. Phycol.* **32**: 207–232.
- , G. G. R. SEATON, C. A. LOVELOCK, AND A. W. D. LARKUM. 1996. Photoinhibition of photosynthesis on a coral reef. *Plant Cell Environ.* **19**: 825–836.
- GENTY, B., J. M. BRIANTAIS, AND N. R. BAKER. 1989. The relationship between quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. *Biochem. Biophys. Acta* **990**: 87–92.
- GLEASON, D. F., AND G. M. WELLINGTON. 1993. Ultraviolet radiation and coral bleaching. *Nature* **365**: 836–838.
- GORBUNOV, M. Y., Z. S. KOLBER, M. P. LESSER, AND P. G. FALKOWSKI. 2001. Photosynthesis and photoprotection in symbiotic corals. *Limnol. Oceanogr.* **46**: 75–85.
- HANELT, D., K. HUPPERTZ, AND W. NULTSCH. 1993. Daily course of photosynthesis and photoinhibition in marine macroalgae investigated in the laboratory and field. *Mar. Ecol. Prog. Ser.* **97**: 31–37.
- HENLEY, W. J., G. LEVAVASSEUR, L. A. FRANKLIN, S. Y. LINDLEY, J. RAMUS, AND C. B. OSMOND. 1991. Diurnal responses of photosynthesis and fluorescence in *Ulva rotundata* acclimated to sun and shade in outdoor culture. *Mar. Ecol. Prog. Ser.* **75**: 19–28.
- HOEGH-GULDBERG, O., AND R. J. JONES. 1999. Photoinhibition and

- photoprotection in symbiotic dinoflagellates from reef-building corals. *Mar. Ecol. Prog. Ser.* **183**: 73–86.
- IGLESIAS-PRIETO, R., AND R. K. TRENCH. 1994. Acclimation and adaptation to irradiance in symbiotic dinoflagellates. I. Responses of the photosynthetic unit to changes in photon flux density. *Mar. Ecol. Prog. Ser.* **113**: 163–175.
- JONES, R. J., AND O. HOEGH-GULDBERG. 2001. Diurnal changes in the photochemical efficiency of the symbiotic dinoflagellates (Dinophyceae) of corals: Photoprotection, photoinactivation and the relationship to coral bleaching. *Plant Cell Environ.* **24**: 89–99.
- KIRK, J. T. O. 1994. Light and photosynthesis in aquatic ecosystems, 2nd ed. Cambridge Univ. Press.
- KOK, B. 1956. On the inhibition of photosynthesis by intense light. *Biochem. Biophys. Acta* **21**: 234–244.
- KOLBER, Z., O. PRASIL, AND P. G. FALKOWSKI. 1998. Measurements of variable chlorophyll fluorescence using fast repetition rate techniques: Defining methodology and experimental protocols. *Biochem. Biophys. Acta* **1367**: 88–106.
- LESSER, M. P., AND M. Y. GORBUNOV. 2001. Diurnal and bathymetric changes in chlorophyll fluorescence yields of reef corals measured in situ with fast repetition rate fluorometer. *Mar. Ecol. Prog. Ser.* **212**: 69–77.
- MUSCATINE, L. 1980. Productivity of zooxanthellae, p. 381–402. *In* P. G. Falkowski [ed.], Primary productivity in the sea. Plenum Press.
- RALPH, P. J., R. GADEMANN, A. W. D. LARKUM, AND U. SCHREIBER. 1999. In situ underwater measurements of photosynthetic activity of coral zooxanthellae and other reef-dwelling dinoflagellate endosymbionts. *Mar. Ecol. Prog. Ser.* **180**: 139–147.
- SAMSON, G., O. PRÁŠIL, AND B. YAAKOUBD. 1999. Photochemical and thermal phases of chlorophyll *a* fluorescence. *Photosynthetica* **37**: 163–182.
- SCHREIBER, U., W. BILGER, AND C. NEUBAUER. 1994. Chlorophyll fluorescence as a non-intrusive indicator for rapid assessment of in vivo photosynthesis, p. 49–70. *In* E. D. Schulze and M. M. Cladwell [eds.], Ecophysiology of photosynthesis. Springer-Verlag.
- SOKOLETSKY, L., Z. DUBINSKY, M. SHOSHANY, AND N. STAMBLER. In press. Non-meteorological predictive models of solar flux and atmospheric transmittance under weakly-varied climatic conditions. *Int. J. Remote Sensing*.
- WYMAN, K. D., Z. DUBINSKY, J. W. PORTER, AND P. G. FALKOWSKI. 1987. Light absorption and utilization among hermatypic corals: A study in Jamaica, West Indies. *Mar. Biol.* **96**: 283–292.

Received: 24 September 2002

Accepted: 28 February 2003

Amended: 17 March 2003