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Photosynthesis and respiration of hermatypic zooxanthellate Red Sea corals from 5–75-m depth

NOGA STAMBLER,* OREN LEVY, AND LIOR VAKI†
The Mina and Everard Goodman Faculty of Life Sciences, Bar-Ilan University, Ramat Gan 52900, Israel

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ABSTRACT

Hermatypic zooxanthellate corals depend on light for photosynthesis. As such, they will not grow at depths deeper than 100 m. Submersible respirometers were used to monitor changes in oxygen concentration for five corals species, *Favia favus, Fungia scutaria*, *Lobophyllia* sp., *Mycedium* sp., and *Stylophora pistillata*. Variations in chlorophyll concentrations, zooxanthellae cell densities, photosynthesis, and respiration rates were detected in these coral species. Two clusters emerged when correlated with deep water, indicating different populations. The first group was restricted to the surface–40 m depth and the second to the 40–75-m depth. Light intensity for saturating photosynthesis E_k was less than 320 μmol q m^{-2} s^{-1} for all species and decreased with depth for most of them.

Keywords: hermatypic corals, photosynthesis, pigments, depth, Gulf of Elat (Aqaba)

INTRODUCTION

Global distribution of coral reefs is controlled by water temperature and nutrient concentration, limiting reefs to the coastal regions of tropical oceans between 30° N and 30° S. Within this belt of oligotrophic "blue deserts", the local and regional distributions of reefs are determined by salinity, temperature, and sedimentation, whereas the depth limit of reefs and the bathymetric zonation of coral species within reefs are governed by light (see Veron, 2000). As the intensity of underwater light decreases exponentially with depth, the dependence of the symbiotic dinoflagellates (zooxanthellae) on light for photosynthesis generally limits the hermatypic corals (Schumacher and Zibrowius, 1985) to the photic zone, which is usually considered the depth from the surface to a depth of 1% of sea subsurface light level (Gardiner, 1930; Wells, 1957; Dustan, 1982; Wyman et al., 1987). The maximal depth of the reef depends on the attenuation of light at any given locality and can extend as much as 100 m.

Corals can be considered, in part, primary producers due to the photosynthetic activity of their symbiotic algae. Zooxanthellae, like all phytoplankton and algae, are capable of photoacclimation, responding to changes in irradiance by cellular changes facilitating light-harvesting capability. In response to low light: (1) chlorophyll and peridinin levels increase (Stambler and Dubinsky, 2004), (2) dinoxanthin, diadinoxanthin, and β-carotene levels decrease (Titlyanov et al., 1980; Dubinsky et al., 1984), (3) the in vivo, chlorophyll-*a*-specific, spectral average, effective optical cross section a* changes (Stambler and Dubinsky, 2005), and (4) ultrastructural modifications take place, including changes in chloroplast volume, number, and length of thylakoids in the chloroplast (Berner et al., 1987).

Chlorophyll concentration per coral area increased along a gradient of decreasing water clarity from oligo-

*Author to whom correspondence should be addressed.
E-mail: stambln@mail.biu.ac.il
†Lior Vaki died tragically during this study.

trophic offshore reefs toward turbid high-nutrient reefs near the coast (Fabricius, 2006). The increase in chlorophyll concentration per area was either due to increase in zooxanthellae density, increase in chlorophyll per zooxanthellae cell, or a combination of the two (Thieberger et al., 1995).

The increase in chlorophyll per algal cell can increase the light absorption of the coral up to fivefold, from 20% to nearly 100%. This darkening of low-light corals usually occurs with no change in the density of the zooxanthellae (Falkowski and Dubinsky, 1981), although Titlyanov (1991) and Titlyanov et al. (2001) found light-related changes in algal density. Corals can harvest different zooxanthellae species or clades at different depths (Baker, 2003; Warner et al., 2006). Photoacclimation also includes changes in the respiration of the zooxanthellae, their light-utilization efficiency, and the light-saturated rate of photosynthesis (Porter et al., 1984). Light-adapted polyps have higher respiration activity compared to shade-adapted polyps (Ulstrup et al., 2006). While, in some cases, photosynthetic response to irradiance of freshly isolated zooxanthellae was not dependent on genotype (Savage et al., 2002; Warner et al., 2006), in other cases it was (Rowan, 2004). In addition to photosynthesis, coral morphology (Graus and Macintyre, 1976; Anthony et al., 2005), enzymatic activity, translocation rate, calcification, and growth rate also depend on light (Levy et al., 2006a,b). Therefore, the adaptation of corals to depth might be the result of symbiotic response, host response, and, presumably, both associations (Falkowski and Dubinsky, 1981; Barnes and Chalker, 1990).

The bathymetric distribution of reef corals shows diversity, first increasing with depth (1 to about 15 m) then decrease in the number of species with increasing depth, which correlates to the decrease in light (Stoddart, 1969; Titlyanov and Latypov, 1991). Loya (1972, 2004) described the community structure and species diversity of the hermatypic corals in Elat down to 30 m. Many species grow at depths deeper than 30 m but few studies have been done on them. The deepest-recorded depth for a zooxanthellate scleractinian coral in the Red Sea is for *Leptoseris fragilis* (Fungiina: Agarciidae), which inhabits the upper twilight zone of 100–145 m (Schlichter et al., 1986). These authors suggest that deep-sea corals provide the zooxanthellae with additional light by transforming short wavelengths into wavelengths suitable for photosynthesis using fluorescent proteins mostly known as GFPs, and by directing light towards algal cells by specialized skeletal structures. Mass et al. (2007) studied the photoacclimation of *Stylophora pistillata* to depth and found that morphology changes are part from their photoacclimation.

Reef corals form effective mechanisms of adaptation and acclimation that have ensured their survival for millions of years (Buddemeier and Smith, 1999; Baker, 2003), but during the last decade, various stresses have caused the degradation of coral reefs (Dubinsky and Stambler, 1996; Hoegh-Guldberg, 1999; Bellwood et al., 2004; Hoegh-Guldberg et al., 2007). The aim of this study was to learn about the physiological ability of different hermatypic coral species under natural conditions from shallow to deep (75 m) waters to understand their physiological acclimation, adaptation, and flexibility.

MATERIALS AND METHODS

Environmental conditions in the Red Sea

The coral reef of Elat is exposed to high sunlight intensities, PAR (photosynthetic available radiation, 400–700 nm), of up to 1500–2000 μmol photons m^{-2} s^{-1} at the surface at noontime. In the study area, light at 75–85 m corresponded to 1% of the light at surface irradiance, depending on the distance from land and phytoplankton concentrations. The light percentage from the surface is based on an attenuation coefficient, Kd, of 0.054 m^{-1} (Stambler, 2006).

The Gulf of Aqaba is characterized by waves less than 0.5 m most of the year. The salinity (~40.6‰), temperature (~20–25 ºC), and nutrients (nitrate <0.01 μM, phosphate <0.01 μM, and silicate <0.1 μM) in the whole water column were almost constant compared to the exponential decrease of light intensity (Stambler, 2006). From this, we assumed that pressure and light are the major variations to which the coral is exposed. Food availability can differ between shallow and deep water but was not measured.

Colony collection

Colonies of the hermatypic corals *Favia favus* (n = 3), *Fungia scutaria* (n = 4), *Lobophyllia* sp. (n = 2), *Mycedium sp*. (n = 8), and *Stylophora pistillata* (n = 2) (ca. 5 cm in diameter) were obtained from several depths on the reef at the Interuniversity Institute for Marine Sciences of Eilat (The H. Steinitz Marine Biology Laboratory) in the Gulf of Aqaba (Elat, Israel). The corals were collected by scuba diving from depths of 5–75 m. The colonies were collected from the maximal light intensity at the depths in which they were grown. The number of samples was limited since the area is a protected nature reserve. The corals collected represent different morphologies but the samples (sub-colonies) we studied were more or less the same size.

Zooxanthellae located deep within a polyp are exposed to lower irradiance compared to those located close to the coral surface (Ralph et al., 2005). Each part

of the colony will respond to light variation differently, but the survival of the whole coral, as a colony organism with connections among all the polyps, is the mean adaptation. As such, studies focusing on small parts of the organisms, for example, studies of fragments, nubbins, or use of micro-electrode or fiber-optic probes might ignore the complex ability of the whole colony. In the present study, we chose relatively big parts of colonies that represent all the variations within the colony. All measurements, including the physiological ones, were taken on the day of collection.

Photosynthesis and dark respiration

The oxygen flux data in situ were obtained using twin, three-chamber, submersible respirometers (AIMS, Australia). The respirometer deployments were performed at a depth of 4–5 m for 24 h, at the collection area in front of the H. Steinitz Marine Biology Laboratory. The respirometer was equipped with UV transparent chambers, each with an oxygen sensor (Kent EIL galvanic type ABB), one light-meter (Li-Cor 4π) underwater quantum sensor, a temperature probe, and a data logger. A centrifugal pump flushed the water in the chambers at programmable 20-min intervals during deployment. Prior to the incubation period, the colonies were carefully cleaned of epiphytes and other surface debris.

Data processing was performed using the AIMS "Respiro" program for calibrating and normalizing the data. Respiration was measured as oxygen uptake during the initial dark period. Parameters from photosynthesis versus energy (P vs. E) curves such as α (initial slope), P_{max} (maximal photosynthesis rate), E_c (compensation intensity), and E_k (saturation intensity), were calculated from a nonlinear curve-fitting based on theoretical models of hyperbolic tangent equations and inverse quadratic functions (Ben-Zion and Dubinsky, 1988).

Biomass parameters

Tissue homogenate was prepared by removing all tissue with a WaterPik (Johannes and Wiebe, 1970). The volume of the homogenate was measured, and sub samples were taken for determination of (1) zooxanthellae density, from direct counting on a haemocytometer; and (2) chlorophyll *a* concentration, determined spectrophotometrically on a Beckman DU-6 spectrophotometer using 90% acetone as a solvent (Jeffrey and Humphrey, 1975).

Surface area of colonies was measured on a Delta-T area meter after the tissue-free skeleton was broken up to avoid overlapping of colony branches. Total surface area was calculated from the projected area multiplied by π, assuming a subcylindrical geometry of the branches (Falkowski and Dubinsky, 1981).

Statistical analysis

Regression, one-way ANOVA (analysis of variance) with Bonferroni and Tamhane, Post Hoc tests, and *t*-test were applied to evaluate variation among treatments (*p* values). The SPSS computer program, version 11.0 (Norusis, 1999), was used for all statistical analyses.

RESULTS

Chlorophyll concentration and zooxanthellae density

Chlorophyll per cm^2 significantly increased in the five species in response to depth increase and light decrease ($p < 0.05$, $R^2 = 0.7$, Fig. 1a). Chlorophyll concentration per cell did not show this pattern in all the colony species ($p > 0.05$). Chlorophyll per algal cell almost doubled in *Fungia scutaria*, while the deepest colony had almost 3 times more chlorophyll compared to the shallowest colony in *Favia favus* (Fig. 1b).

There was an increase in cell algae per area with depth in the species *Lobophyllia* sp., *Mycedium* sp., and *Stylophora pistillata*, while there was no change in algal density in *Favia favus* and *Fungia scutaria* ($p > 0.05$, Fig. 1c).

Respiration and photosynthesis parameters

The respiration rate of the corals varied between species and depth. The respiration rate per area increased with depth in *Favia favus* and varied with depth in the other four species. There was no significant correlation between metabolism per coral area, per chlorophyll, or per cell with depth ($p > 0.05$, Fig. 2a,b). Even though corals from the 40–75-m depth had higher chlorophyll per cm^2 compared to shallow corals, their respiration rate per area was not significantly different ($p > 0.05$) either for chlorophyll or algal cell basis (data not shown). The respiration rate per chlorophyll decreased exponentially ($r^2 = 0.4$) with chlorophyll per algal cell (Fig. 2c).

Compensation light levels (E_c), saturation intensity (E_k), the initial slope per chlorophyll (α), and the maximal photosynthesis rate (P_{max}), changed between species and were not function of depth (data not shown). E_c, E_k, and P_{max} correlated as a function of chlorophyll concentrations and cell densities (Fig. 3). The ratio between photosynthesis and respiration decreased at a depth between the surface and 30 m; the opposite was true at a depth between 30 and 80 m (Fig. 4).

DISCUSSION

Coral reefs develop at the surface-to-deep-water depth (~100 m). The shallow water reef is characterized by

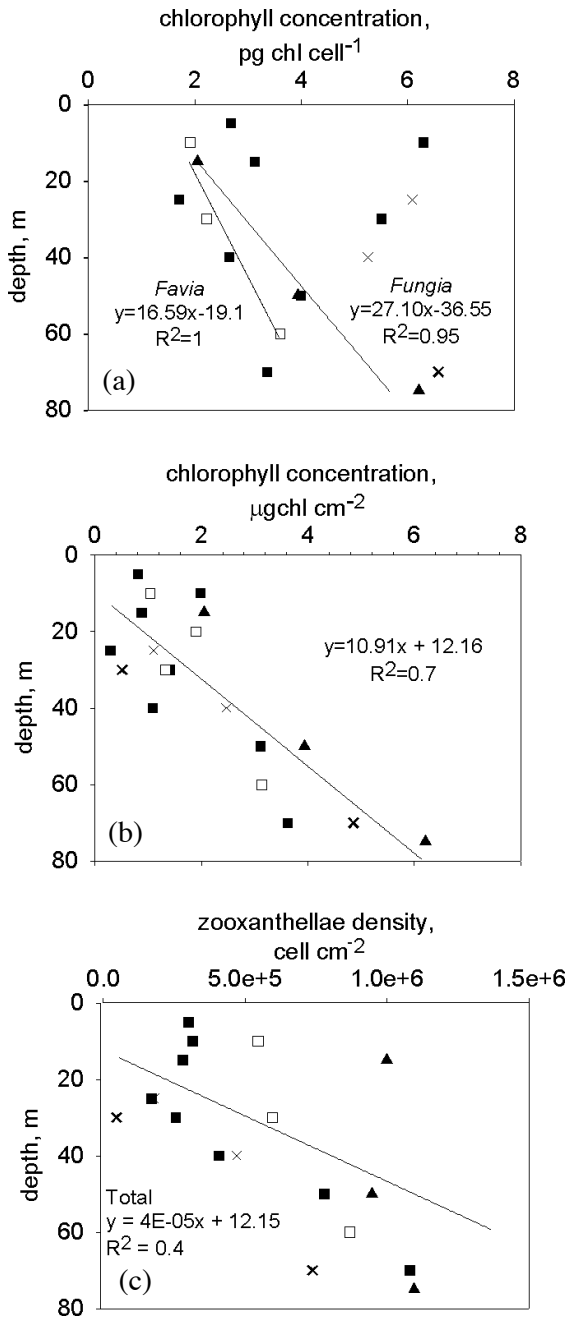

Fig. 1. Chlorophyll concentrations and algal cell density as functions of depth for the corals: *Favia favus* (▲), *Fungia scutaria* (◆), *Lobophyllia* sp. (×), *Mycedium* sp.(■), and *Stylophora pistillata* (×). (a) chlorophyll concentrations per area; (b) chlorophyll concentrations per algal cell; and (c) algal cell density.

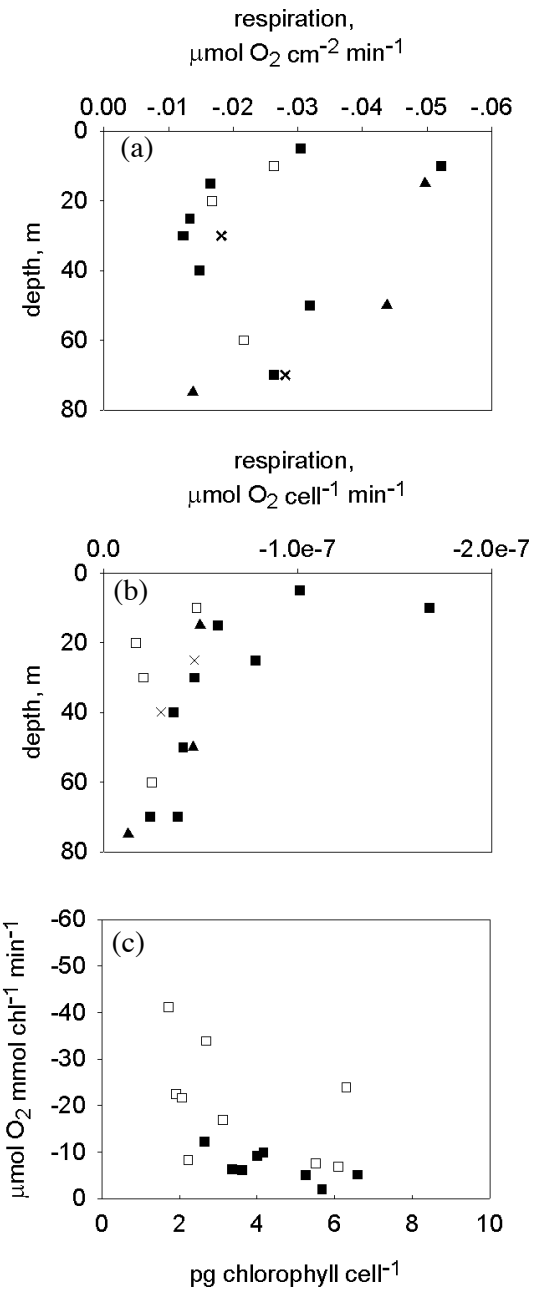

Fig. 2. (a) Respiration per coral area as function of depth for the corals *Favia favus*, *Fungia scutaria*, *Lobophyllia* sp., *Mycedium* sp., and *Stylophora pistillata* (symbols as in Fig. 1); (b) respiration per cell as function of depth (symbols as in Fig. 1); (c) respiration per chlorophyll as function of chlorophyll per cell, 0–30 m (□), 40–75 m (■).

high diversity and density compared to the deep water reef (Stoddart, 1969; Loya, 1972; Veron, 2000). Coral variations are an outcome of genetics and environmental factors such as latitude (Veron, 2000). Coral photosynthesis and physiology depend on photoacclimation and photoadaptation.

Red Sea corals at 75 m were exposed to ~2% of surface light rich with blue spectra compared to shallow-water corals (Stambler, 2006). These deep corals were acclimated to low light intensities by increasing their absorption pigments (Fig. 1a). The increase in chlorophyll per area was due to the increase in chlorophyll per algal cell in the cases of *Fungia scutaria* and *Favia favus* (Fig. 1b), while in *Mycedium* sp., the increase in chlorophyll was due to an increase in algal densities (Fig. 1c). Both strategies are well known from other studies (e.g., Wyman et al., 1987; Titlyanov et al., 2001). Response to light intensity by algae was initiated by changing the pigment concentration; the daily variation in light affects the pigment concentration (Levy et al., 2006b). Growing under low light intensity will reduce the energy available to the algae; theoretically, this should reduce the algae growth rate and, as such, the algae density. However, since the zooxanthellae density at the coral tissue is balanced by the coral and the flow of nitrogen in ratio to carbon, the algae density increases (Falkowski et al., 1993). As such, these acclimations depend on the coral species, its morphology, and other conditions including nutrient concentration and zooplankton availability (Houlbreque et al., 2003; Klaus et al., 2007). Similar to *Fungia scutaria* and *Favia favus* (Fig. 1b), chlorophyll concentrations per algal cell at Discovery Bay, Jamaica, for the corals *Acropora agricites, Montastrea annularis, Montastrea cavernosa*, and *Porites astreoides* were greater for zooxanthellae growing in low light (30–50 m) than for those growing

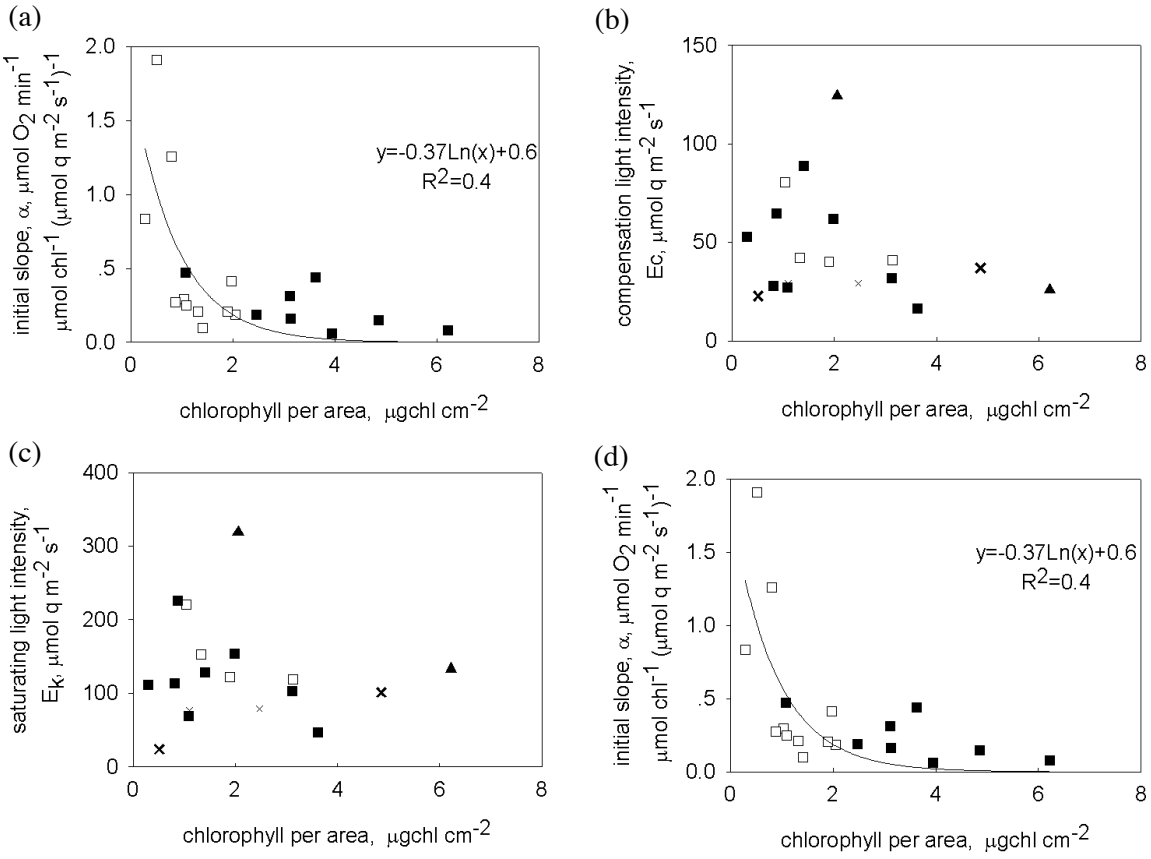

Fig. 3. (a) Maximum photosynthesis per chlorophyll as function of chlorophyll per area, for the corals *Favia favus*, *Fungia scutaria*, *Lobophyllia* sp., *Mycedium* sp., and *Stylophora pistillata* (symbols as in Fig. 1); (b) compensation light levels, E_c, as function of chlorophyll per area; (c) saturating light intensity, E_k, as function of chlorophyll per area; and (d) the initial slope, α, per chlorophyll as function of chlorophyll per area (0–30 m (□), 40–75 m (■).

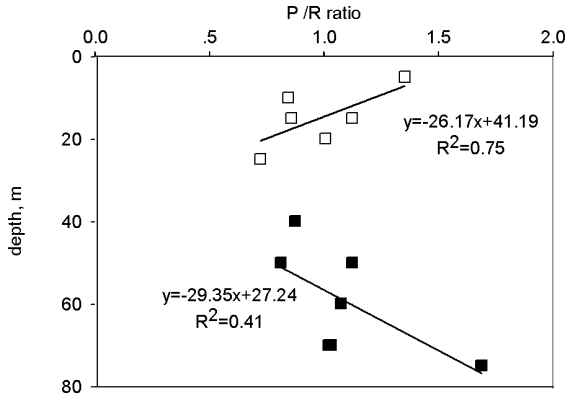

Fig. 4. Ratio between maximum photosynthesis rate and respiration, as function of depth.

at higher light intensities in shallow water (1–10 m) (Wyman et al., 1987). Wyman et al. (1987) found that even though concentration per cell increased—usually systematically—with depth, the significant variation was between 30–50 m compared to 1–50 m. This is similar to the response of corals grown in our study at a depth <40 m (Figs. 2–4). The maximum electron transport rates (ETR) of *Montastraea faveolata* from a 30 m depth at Carrie Bow, Cay, Belize, was much lower than other depths (Lesser, 2004).

It should be noted that a higher increase in cell density is not efficient since the zooxanthellae will have to be arranged in more than one layer. Assuming that the algae are spheres with a radius of 10–13 μm, the maximal number of algae in 1 cm^2 of coral is ~1–1.5 10^6, causing a shading or "package effect". For the same reason, a greater increase in chlorophyll per cell will result in a "package effect" (e.g., Stambler and Dubinsky, 2005). The zooxanthellae corals at 75 m are extremely dark, having absorbed maximum light, like a black body (Dubinsky and Jokiel, 1994). As they cannot become much darker than that, they cannot grow at much deeper depths. Corals grown in complete darkness will lose their zooxanthellae (Dubinsky and Jokiel, 1994; Anthony and Hoegh-Guldberg, 2003a); in case there will be some zooxanthellae they will lose their pigments and will not photosynthesize (Grant et al., 2004). Only a few tropical zooxanthelate corals such as *Plesiastrea versipora* may survive without the zooxanthellae under feeding conditions (Grant et al., 2004).

Maximum photosynthetic rate (P_{max}) is highest for shallow corals from Jamaica (Wyman et al., 1987), the Great Barrier Reef (Chalker and Dunlap, 1983), and the Red Sea, which explains the development of the reef in shallow water. Photoacclimation to light variability is mainly by changes in saturating light intensity for photosynthesis (E_k), as shown for *Turbinaria mesenterina* (Anthony and Hoegh-Guldberg, 2003b). E_k in the present study was less than 320 μmol photons m^{-2} s^{-1} for all species and decreased with depth, with the exception of *Lobophyllia* sp. (Fig. 4). Similar values were found for *Stylophora pistillata* (Mass et al., 2007). The decrease with depth was comparable to the reduction (from 169 at 1 m to 22.9 μmol photons m^{-2} s^{-1} at 80 m) for *Acropora* spp. from the Great Barrier Reef (Chalker and Dunlap, 1983). As the shallow (0–30 m) coral in the Gulf of Elat was exposed throughout the year to more than 100 μmol photons m^{-2} s^{-1}, they always reached their minimum E_k.

The efficiency of photosynthesis, the initial slope (α) of the Red Sea corals was 0.007–0.169 μg O_2 μg chl $^{-1}$ h^{-1} (μmol photons m^{-2} $s^{-1})^{-1}$, which is in the range found for Jamaican coral (0.010–0.275 μg O_2 μg chl $^{-1}$ h^{-1}), with variations among species (Wyman et al., 1987). In shallow water, higher values were found for the Red Sea corals, although there was no significant variation based on species level ($p > 0.05$). In another study, the efficiency of photosynthesis of *Stylophora pistillata* from the Red Sea increased with depth (Mass et al., 2007). In contrast, in Jamaica, only *Porites astreoides, Agaricia agricites*, and *Montasterea annularis* showed an increase with depth (Wyman et al., 1987).

Red Sea coral colonies showed diverse respiration rates, with higher values in shallow (0–30 m) water (Fig. 2). At the Great Barrier Reef, as depth increased from 1 to 80 m, *Acropora* spp. respiration decreased (Chalker and Dunlap, 1983). Diel P/R ratio reached a maximum at 30 m and declined rapidly deeper than 40 m (Chalker and Dunlap, 1983). Opposite trends were observed in the P/R ratio in this study (Fig. 4). These differences might result from variations in zooplankton availability and nutrient concentrations that can influence colony respiration. While the variation in photosynthesis is due to zooxanthellae fixation, the major fraction of the respiration is due to the host respiration. Shallow water corals exposed to high light intensity might obtain up to 100% of their respiratory demands from algal photosynthesis as compared to 40% in shade-adapted ones (Falkowski et al., 1984; Muscatine et al., 1984; Edmunds and Davies, 1986). As we cannot separate the respiration of the algae and the animal, we can only assume that the changes in respiration are due to both the coral itself and the zooxanthellae.

Falkowski et al. (1990) found that for each coral species, there can be an optimal depth for light harvesting, especially since different species growing at the same depth can be expected to differ in their light harvesting. As a result of the environmental conditions and acclima-

tions/adaptations, species are diverse with depth in the Red Sea as well as in other reefs (Loya, 1972; Veron, 2000). *Mycedium* sp. is the most widespread species and can be found at almost any depth, even though few colonies were found at each depth. The colony shape of this species allows it to grow under low light intensities (see Vermeij and Bak, 2002). In spite of the coral's ability to adapt and acclimate to deep water, the reef developed in the shallow water because there is more sun energy available there. Under natural conditions, corals have an advantage growing in the deep waters, while shallow corals are well adapted to growth closer to the surface, e.g., with higher light and P_{max} (Fig. 3). There is a reduction in the efficiency of light use for photochemistry by zooxanthellae under high light intensities (Winters et al., 2003), although respirometer data on coral metabolism in shallow waters do not indicate any photoinhibition during the midday hours (Levy et al., 2006a). Hoogenboom et al. (2006) show that even though the daily costs of photoinhibition are negligible, the photoacclimation to high light levels reduces daily energy acquisition in the long term, primarily due to decreased chlorophyll concentrations. The maximum rates of electron transport rates (ETR) depress at higher irradiances with coral growth depth (Lesser, 2004). Nonphotochemical quenching and maximum excitation pressure over PSII (Qm) decreased with depth from 2 to 25 m (Warner et al., 2006). The physiological differences did not depend on the symbiont clades occurring in the same species of coral at a particular depth or on the coral species (Warner et al., 2006). Corals from the Red Sea have zooxanthellae *Symbiodinium* clades A and C (Karako-Lampert et al., 2004). Lampert-Karako et al. (2008) show that shallow water colonies (5 m) of *Stylophora pistillata* harbor clade A while deeper-water colonies (17 m) harbor either clade A or C. We did not examine zooxanthellae clade diversity in corals in the present study, however, we also did not find significant variation between the coral species ($p > 0.05$) that might or might not have had different clades in their tissue.

The corals in our study represent various basic coral morphology—from the flat solitary coral *Fungia scutaria* to the colonies of the laminar encrusting coral *Mycedium* sp., the hemispherical colony of *Lobophyllia* sp., the spherical coral *Favia favus*, and the branch coral *Stylophora pistillata*. The size of the polyp of the studied corals varied from very large (*Fungia* ~150 mm) to as small as 4 mm (*Mycedium*). These differences among the coral species are thought to have an influence on the ability of the coral to capture zooplankton positively correlated with coral polyp size; heterotrophic coral will have larger polyps (Porter, 1976). However, Sebens et al. (1996) show that the success at capturing zooplankton does not depend on polyp size. Palardy et al. (2005) found increased feeding rates with increasing depth, with no correlation to polyp size. Heterotrophic feeding does not balance the decrease in energy captured by photosynthesis when irradiance decreases with depth (Wellington, 1982). As a response to light decrease with depth, spherical corals such as *Favia* sp. can increase their size (Stambler and Dubinsky, 2005). Unlike spherical and encrusting species, increasing colony size of branching corals such as *Stylophora pistillata* and *Acropora* sp. will enhance self-shading among branches. The branched corals change their shape to a more flattened and horizontal morphology (Goreau and Goreau, 1959; Roos, 1967; Dustan, 1982; Fricke and Schuhmacher, 1983; Stambler and Dubinsky, 2005; Mass et al., 2007).

Our study shows that in spite of the different conditions between the surface and deep water, down to 75 m, the physiology of the corals is similar and as such, deep corals can photosynthesize under low and high light intensities.

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