The Journal of Experimental Biology 213, 4084-4091

doi:10.1242/jeb.039891

The spectral quality of light is a key driver of photosynthesis and photoadaptation in *Stylophora pistillata* colonies from different depths in the Red Sea

T. Mass[1,2,*], D. I. Kline[3,*,†], M. Roopin[4], C. J. Veal[3], S. Cohen[2], D. Iluz[4,5] and O. Levy[4]

[1]Evolution Systematics and Ecology Department, Life Sciences Institute, The Hebrew University of Jerusalem, Jerusalem 91904, Israel, [2]The Interuniversity Institute for Marine Sciences, H. Steinitz Marine Biology Laboratory, PO Box 469, Eilat 88103, Israel, [3]Global Change Institute, Coral Reef Ecosystems Laboratory, The University of Queensland, St Lucia, Queensland 4072, Australia, [4]The Mina and Everard Goodman Faculty of Life Sciences, Bar-Ilan University, Ramat-Gan 52900, Israel and [5]The Department of Geography and Environment, Bar-Ilan University, Ramat-Gan 52900, Israel

*These authors contributed equally to this work
†Author for correspondence (d.kline@uq.edu.au)

Accepted 16 September 2010

SUMMARY

Depth zonation on coral reefs is largely driven by the amount of downwelling, photosynthetically active radiation (PAR) that is absorbed by the symbiotic algae (zooxanthellae) of corals. The minimum light requirements of zooxanthellae are related to both the total intensity of downwelling PAR and the spectral quality of the light. Here we used *Stylophora pistillata* colonies collected from shallow (3 m) and deep (40 m) water; colonies were placed in a respirometer under both ambient PAR irradiance and a filter that only transmits blue light. We found that the colonies exhibited a clear difference in their photosynthetic rates when illuminated under PAR and filtered blue light, with higher photosynthetic performance when deep colonies were exposed to blue light compared with full-spectrum PAR for the same light intensity and duration. By contrast, colonies from shallow water showed the opposite trend, with higher photosynthetic performances under full-spectrum PAR than under filtered blue light. These findings are supported by the absorption spectra of corals, with deeper colonies absorbing higher energy wavelengths than the shallow colonies, with different spectral signatures. Our results indicate that *S. pistillata* colonies are chromatically adapted to their surrounding light environment, with photoacclimation probably occurring *via* an increase in photosynthetic pigments rather than algal density. The spectral properties of the downwelling light are clearly a crucial component of photoacclimation that should be considered in future transplantation and photoacclimation studies.

Key words: photoadaptation, transplantation, chromatic adaptation, coral, absorption spectra.

INTRODUCTION

Coral reefs are highly productive ecosystems that support a large diversity of biological activity (Hoegh-Guldberg, 1999; Hughes et al., 2003; Yentsch et al., 2002) and are capable of fixing six times the amount of carbon than the phytoplankton in the surrounding oligotrophic water mass (Crossland et al., 1991). The success of coral reefs in these nutrient-poor waters is achieved through a mutualistic symbiosis of the host coral with photosynthetic dinoflagellates, *Symbiodinium* spp., known as zooxanthellae. The zooxanthellae are found within the membrane-bound vacuoles of cells within the host coral, close to the cell–water interface (Glynn, 1996). These symbionts are capable of utilizing vast quantities of the downwelling light energy incident on the coral, of which up to 95% of the resultant organic carbon is translocated to the host for respiration and growth (Muscatine, 1990). The light dependence of zooxanthellae plays a major role in controlling the bathymetric distribution of corals (Schuhmacher and Zibrowius, 1985). Hermatypic, or reef-building, corals are generally limited to the euphotic zone, which is defined as depths with greater than 1% of the sea subsurface light level (Dustan, 1982; Wells, 1957). The maximal depth of the reef depends on the attenuation of light in any given locality and may extend as deep as 100 m.

The aquatic light environment has a major influence on the productivity, physiology and ecology of reef-building corals (Dubinsky et al., 1984; Dustan, 1982; Falkowski et al., 1990; Porter et al., 1984). Underwater light decreases exponentially with depth, roughly following the Beer–Lambert law (Gordon, 1989). The exponential reduction in aquatic light intensity with depth is partly attributed to the absorbing properties of the water itself (Smith and Baker, 1981) but the majority of absorption and attenuation is caused by dissolved organic material and suspended sediments in the water column. The seasonal abundance of phytoplankton also has a significant influence on the downwelling irradiance light field. However, in the nutrient-poor waters where coral reefs are most abundant, phytoplankton density is usually quite low (Genin et al., 2009; Houlbreque et al., 2006; Yahel et al., 1998). Light attenuation is not uniform over all wavelengths, and the water column behaves like a monochromator, narrowing the spectrum of the most-penetrating light to a relatively narrow waveband (Falkowski et al., 1990; Jerlov, 1968; Jerlov, 1976). In the clear, tropical waters surrounding reefs, light extinction in the violet and blue wavelengths is minimal, with higher attenuation occurring at longer wavelengths.

The Gulf of Eilat, Red Sea, has unusually clear water with high light levels throughout the year, even at depth. Winters et al. compared the surface light levels measured in Eilat over an 8-year period to those measured on three other reefs globally during the same period (1990–1998; Heron Island, Queensland, Australia; Puerto Morales, Quintana Roo, Mexico; and Coconut Island, Kane'ohe Bay, Hawaii) and found that light levels in Eilat were over 40% higher than on any of the other reefs (Winters et al., 2009). One possible reason for these high light levels in Eilat are the uniformly clear, blue skies, with minimal cloud cover throughout

the year, that are characteristic of this desert environment. Surface global solar radiance regularly reaches 7500 W m^{-2} day^{-1} in summer and 3500 W m^{-2} day^{-1} on clear winter days (Stambler, 2006). The waters themselves are transparent, with no river sediment inputs, and are characterized by euphotic depths of 80 to 120 m. Furthermore, the oligotrophic Gulf supports only scant phytoplankton communities with low chlorophyll *a* (chl *a*) concentrations ranging between a summer minimum of 0.2 μg l^{-1} chl *a* and a winter peak of 0.6 μg l^{-1} chl *a* (Iluz et al., 2003; Stambler, 2006), but with exceptionally high values of 1.5 μg l^{-1} chl *a* measured in the spring of 2008 (Iluz et al., 2009). These properties clearly place the Gulf of Eilat in Morel and Prieur's (Morel and Prieur, 1977) case 1 water types (Iluz, 1998; Stambler, 2006). The environmental light field in the Gulf of Aqaba is a key factor impacting the physiology of the corals and their associated symbionts.

Zooxanthellae, like all phytoplankton and algae, are capable of photoacclimation to different light regimes. Photoacclimation can include cellular changes that optimize their light harvesting and utilization capabilities, such as increasing their chlorophyll and peridinin concentrations, thereby increasing the light absorptivity of the coral up to fivefold (Dubinsky et al., 1984; Mass et al., 2007; Porter et al., 1984; Titlyanov et al., 2001). Furthermore, ultrastructural modifications in response to light intensity can occur, including changes in the chloroplast volume and in the number and length of the thylakoids within the chloroplasts (Dubinsky et al., 1984; Stambler, 1998). Photoacclimation can also include changes in the respiration, light utilization efficiency or light-saturated rate of photosynthesis of the zooxanthellae (Porter et al., 1984). Additionally, low-light corals often have darker tissues owing to increased pigmentation without a change in the density of the zooxanthellae (Falkowski and Dubinsky, 1981; Falkowski et al., 1984; Mass et al., 2007), although Titlyanov did find light-related changes in algal density (Titlyanov, 1991; Titlyanov et al., 2001).

Corals contain a diverse array of host pigments, many of which, such as the green fluorescent proteins, are crucial to their light-absorption capabilities (Alieva et al., 2008; D'Angelo et al., 2008). D'Angelo et al. found that an increase in coral pigmentation was dependent on the spectral quality of the light, with blue light levels being the key driver of pigment concentrations (D'Angelo et al., 2008). Another interesting group of proteins recently discovered in the coral host are the blue-light photoreceptor proteins known as cryptochromes (Levy et al., 2007). These proteins probably use blue monochromatic light as an external time-keeping cue to entrain the core circadian clock mechanism to its environment.

Plants and algae use chromatic acclimation to optimize their light harvesting and utilization abilities in response to spatial and temporal changes in underwater irradiance (Falkowski and LaRoche, 1991). This is a well-known phenomenon in algae physiology that was first discovered in the late 19th to early 20th century by Engelmann and Gaidukov from their work on blue-green algae (genera *Oscillaria* and *Phormidium*) cultivations under different light spectra (Engelmann and Gaidukov, 1902). Their study showed that algae efficiently absorb light in response to the selective accumulation of pigments complimentary in color to the spectral composition of the incoming radiation when exposed to radiation of poor spectral composition for a long period (Engelmann and Gaidukov, 1902). Chromatic acclimation has been also conclusively demonstrated in cyanobacteria as well as in brown and red algae that can dramatically change their pigmentation complex (Grossman, 2003). In other presumed instances of chromatic acclimation, it has been suggested that these are likely to be cases of photoacclimation rather than wavelength acclimatization (Dring, 1989; Schmid and Dring, 1996).

Here we attempt to evaluate the performance of diel changes in photosynthesis and respiration in the coral *Stylophora pistillata* (Esper, 1797) by measuring oxygen flux under different light spectra. Photosynthetic performance was compared using colonies from deep (40 m) and shallow (3 m) depths that were subjected to two light regimes: a full photosynthetically active radiation (PAR) spectrum of 400–700 nm and a blue light spectrum (380–460 nm). Coral visible light reflectivity measurements were performed to compare the spectra of light absorbed by the deep and shallow corals. Additionally, the spectral irradiance of the water column to a depth of 100 m was measured during the experiment to verify that our experimental light spectra were similar to those occurring in the field.

MATERIALS AND METHODS

Study site and coral sampling

Branches of *Stylophora pistillata* (Esper 1792) were collected under a special permit from the Israeli Natural Parks Authority in the waters in front of the H. Steinitz Marine Biology Laboratory, Eilat, Israel, Red Sea (29°30′N, 34°56′E), using SCUBA diving. *S. pistillata* was chosen as an experimental organism because it is a common, widely distributed, hermatypic, branching coral that has been extensively studied. It is known as an opportunistic (r-strategist), stress-tolerant species that inhabits a range of reef environments from the shallow reef flat (2 m) to over 70 m depth (Loya, 1976).

Three branches, 10–15 cm long, were collected from three different colonies (mean colony diameter of 30 cm) that were at least 25 m apart along a 100 m line transect at both shallow (3 m) and deep depths (40 m). The colony morphology at the two depths was similar to that described in a previous study from this reef (Einbinder et al., 2009). Shallow colonies had a mound-like shape with thicker branches whereas deep colonies were flatter with thinner branches. The collected branches were placed in a black container that was carried to a shaded short-term incubation area in a water table with flow-through seawater. Light intensity in the water table was adjusted to match light levels at the collection depths, where irradiance was ~90% (3 m) and ~10% (40 m) of the light levels at the surface. This shading accounted for the overall PAR but could not correct for the changes in the light spectrum that exist between deep and shallow waters. However, the corals were only maintained under these conditions for, at most, a few hours and were subsequently placed in the respirometer. Comparison of photosynthesis under full light spectra (PAR) with blue light spectra was achieved using a neutral density filter [neutral density 210 (0.6) 20% transmission; Lee Filters, Andover, UK] and blue filter (400–500 nm, deep blue 120, 40% transmission; Lee Filters) to ensure the same light intensity for both treatments. Light measurements were obtained with a Diving PAM (Walz, Effeltrich, Germany) light meter probe.

In addition to the corals used in the respirometer experiment, 20 *S. pistillata* branches were collected for absorbance measurements: 10 branches each were collected from both 40 and 3 m, from 20 different colonies (10 shallow, 10 deep) along a 100 m line transect at each depth, with the individual colonies approximately 10 m apart. These samples were transported from depth in a black box and kept in total darkness for 30 min prior to the absorption measurements.

Photosynthesis and dark respiration

Oxygen flux data were obtained using a three-chamber submersible respirometer [Australian Institute for Marine Science (AIMS),

Townsville, Australia]. The instrument is equipped with three UV-transparent chambers, with oxygen sensors (EIL galvanic type ABB; Kent Scientific Corporation, CT, USA), a light meter (LI-192 underwater quantum sensor; Li-Cor Biosciences, Cambridge, UK), a temperature probe and a data logger (Levy et al., 2004). A centrifugal pump flushes the water in the chambers at programmable intervals, with 20 min intervals used for these experiments (Fabricius and Klumpp, 1995; Levy et al., 2004). Prior to the incubation period, the colony surfaces were carefully cleaned of epiphytes and other debris. The respirometer was deployed under natural light in a 1 m deep tank in the H. Steinitz Marine Biology Laboratory. Flow speeds of 4 ml min^{-1} were obtained within the chambers with stirring motors. Due to logistic and permit limitations, only three replicate corals could be used in each run of the respirometer and the deep and shallow treatments were only performed once.

Data were processed using the AIMS 'Respiro' program for calibrating and normalizing the data. Respiration was measured as oxygen uptake during the nighttime periods. The increase in respiration after sunset, an effect known as enhanced post-illumination respiration (EPIR), was also observed and quantified. Parameters from the photosynthesis (P) versus energy (E) curves, including initial slope (α), maximal photosynthesis rate (P_{max}), compensation light levels (E_c), optimum irradiance (E_{opt}), compensation intensity (I_c) and saturating intensity (I_k) were calculated from a non-linear, empirical curve based on hyperbolic tangent equations (Benzion and Dubinsky, 1988). At the end of the experiments the colonies were cleaned of living tissue using an airbrush, soaked in freshwater and dried. The surface areas of the corals were then determined using the paraffin method as previously described (Stimson and Kinzie, 1991). The oxygen electrodes of the respirometer were calibrated at 25°C in air-saturated and zero concentration (prepared with sodium sulfate) seawater and the measurements were checked during the experiment with the Winkler titration method (Winkler, 1888; Carpenter, 1965).

Zooxanthellae isolation and protein assay

After measuring photosynthesis of the intact coral, the tissue was removed with an airbrush using a reservoir of 0.20 µm filtered seawater. The volume of homogenate and the concentrations of zooxanthellae cells per unit volume of homogenate were determined in order to standardize the absorption and biomass data. The density of zooxanthellae in the homogenate was determined by microscopic counts in a hemocytometer with 10 replicate cell counts per sample. The total protein content in the tissue was determined using the Bradford method (Bradford, 1976). Total protein to surface area ratios were calculated to represent changes in coral biomass. Chl *a* was extracted in cold acetone (90%) overnight. Chl *a* concentrations were determined spectrophotometrically according to the equations of Jeffrey and Humphrey (Jeffrey and Humphrey, 1975), using an Ultraspec 2001 Pro spectrophotometer (Biochrom Ltd, Cambridge, UK). Based on homogenate volumes, acetone volumes, coral area and zooxanthellae counts, both µg chl *a* cm^{-2} of coral and pg chl *a* $zooxanthella^{-1}$ were calculated.

Coral visible light reflectivity

Coral reflectivity measurements were undertaken using a methodology adapted from Enriquez et al. (Enriquez et al., 2005) and Hochberg et al. (Hochberg et al., 2006). After 30 min of dark adaptation, coral fragments were removed from their seawater-filled darkened storage container, toweled dry and then placed on a matte black surface inside a dark room. Coral reflectance measurements were made with an Ocean Optics USB 2000 spectrophotometer (Ocean Optics Inc., Dunedin, FL, USA), with a visible and infrared optimized transmission fiber. Each coral fragment was illuminated by a visible light Schott KL 2500 optic fiber (Schott, Mainz, Germany), located 45 deg to the horizontal, 20 mm from the coral fragment. The reflected signal was collected from a 10 mm^2 section of the coral by the spectrophotometer's fiber, located orthogonal to the fragment at the same distance from the coral surface. Reflection was measured as the difference between the reflected signals from the coral surface compared to a reflective standard (reflecting 99.99% of visible light). The absorption was calculated as a function of 1 minus the reflected signal. Post-processing of each measurement was performed to remove electrical dark values from the spectrophotometer readings that were generated when there was no input light but when there was still a very minute signal recorded. Second-order derivates of the dark corrected reflectance spectra were then made to investigate absorption bands from both shallow and deep corals (Wettle et al., 2003).

Light measurements

Underwater irradiance measurements were conducted with a Biospherical PRR-800 standard high-resolution profiling reflectance radiometer (Biospherical Instruments Inc., San Diego, CA, USA) with free-falling profiling frame to allow the collection of boat shadow free data. The PRR measures downwelling irradiance along 19 channels in the ultraviolet and visible range of the spectrum centered at 305, 313, 320, 340, 395, 443, 465, 490 520, 560, 589, 665, 683, 694, 710, 765, 780 and 875 nm, as well as a broad-spectrum downwelling PAR channel (EdzPAR, 400–700 nm) and a temperature channel. Three irradiance profiles were determined for the surface to 100 m depth between 11.00 and 16.00 h on 3 April 2008 and the data were recorded directly to a laptop. The euphotic zone depth was calculated from the EdzPAR.

Statistical analysis

Statistical analyses were conducted using SPSS 15.0 (SPSS Inc., Chicago, IL, USA). Normality and homogeneity of variance were examined using the Shapiro–Wilk statistical test for $N<50$. The differences in oxygen evolution among corals from different depths (3 m *vs* 40 m) during two consecutive days with alternative light treatments (blue light *vs* PAR) were tested using a repeated-measures ANOVA (RM-ANOVA) with light treatment as a repeated measure. The tests were followed by pairwise comparisons of estimated marginal means (Bonferroni adjusted). All results were considered significant at $P\leq0.05$ and are presented as means ± 1 s.e., unless otherwise indicated. *Symbiodinium* densities, total protein content and chl *a* concentration of corals from 3 m *vs* 40 m depths that were used for oxygen measurements were compared using independent-sample *t*-tests.

Coral reflectivity measurements were averaged and plotted with s.d. Statistical analysis was conducted using an ANCOVA with treatment plotted against wavelength to determine the statistically significant differentiation of the reflectivity profiles.

RESULTS

Photosynthesis measurements

Diurnal measurements of oxygen flux using the three-chamber submersible respirometer showed an increase in oxygen evolution with light intensity for the deep and shallow *S. pistillata* colonies. The oxygen evolution however, differed between full PAR and blue light (400–500 nm). The shallow water colonies ($N=3$) had higher photosynthetic rates on the first day when exposed to full PAR with a maximum intensity of 370 µmol quanta m^{-2} s^{-1}, compared with the

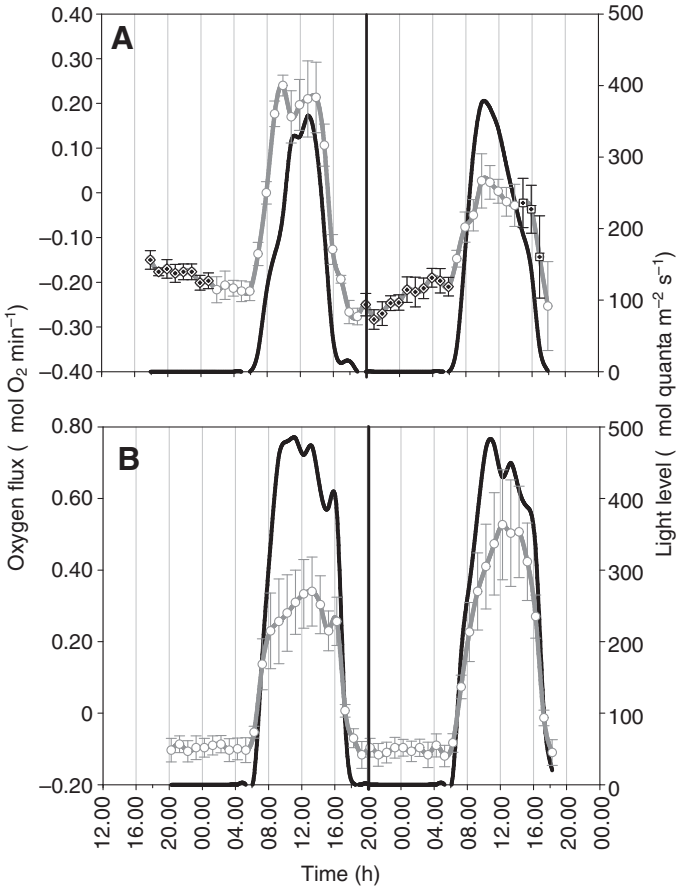

Fig. 1. *Stylophora pistillata* oxygen flux measured under natural photosynthetically active radiation using a respirometer, with oxygen data (grey) and irradiance data (black) displayed. (A) Corals from 3 m depth; (B) corals from 40 m depth. The vertical black lines represent the addition of the blue light filter to the respirometer chambers. Diamonds indicate the section of the oxygen curve where enhanced post-illumination respiration is evident in the shallow colonies; squares indicate the 'lag' ('shift to the right') reverse hysteresis in oxygen flux to the light.

consecutive day in which blue light was used with the same maximum light intensity (Fig. 1A). Photosynthesis under the blue light spectra was over one order of magnitude lower, with oxygen values under the compensation point for most of the day. The ratio of gross photosynthesis to respiration (P_g/R) was 0.83 with blue light and 1.67 with PAR illumination (Table 1). Remarkably, the deep *S. pistillata* colonies (N=3) showed the opposite trend, with higher oxygen production under the blue light spectra with a maximum intensity of 480±5 μmol quanta m^{-2} s^{-1} for both days (Fig. 1B). The P_g/R ratio was 2.12 for the first day under full PAR illumination and 4.31 under blue light during the second day (Table 1). The maximum oxygen production was approximately 150% higher when the same colonies were exposed to blue light *vs* PAR irradiation. The compensation light intensity was similar between the 3 m and 40 m depth colonies under PAR illumination (Table 1). However, the compensation intensity was almost an order of magnitude higher for the shallow corals under blue light (310.24±20.60 μmol quanta m^{-2} s^{-1}) than for the deep-water corals under blue light (32.13±8.66 μmol quanta m^{-2} s^{-1}).

The P_g/R ratio varied significantly with alternative light treatments (RM-ANOVA, $F_{1,4}$=7.66, P=0.05) and with depth (RM-ANOVA, $F_{1,4}$=62.87, P<0.005). Significant interaction between the response in P_g/R to light treatments and coral depth was measured (RM-ANOVA, $F_{1,4}$=40.61, P<0.005). Light quality (blue light *vs* PAR) appeared to make a major contribution to the variation in gross photosynthesis amongst corals from different depths. Thus, in contrast to corals from the same depth, light quality (blue light *vs* PAR) appeared to have contributed to the variation in oxygen evolution rate during the day amongst corals from different depths.

The phenomenon of EPIR was apparent for the shallow colonies (Fig. 1A, diamonds) mostly during the first night. EPIR was pronounced for ~7 h after sunset and decreased later in the night (Levy et al., 2004). The presence of EPIR suggests a history of photosynthesis/respiration during the day with an exposure to a different level of radiation, such as high light. Previous studies have found similar responses in free-living phytoplankton that showed a marked increase in respiration rate following exposure to high light (Beardall et al., 1994; Falkowski et al., 1985). After the decline in EPIR, the respiration rate for all measurements remained almost uniform during the subsequent dark hours until dawn. The deep colonies did not show any signs of the EPIR effect and their respiration remained stable throughout the night (Fig. 1B). Another phenomenon observed that has been previously reported (Levy et al., 2004) is the reverse hysteresis effect, or morning depression, which was realized as higher oxygen evolution in the afternoon than in the morning under the same irradiance levels. Reverse hysteresis was observed in the shallow corals only under blue light, as seen from the time-phase data, with increased photosynthetic rates in the afternoon (Fig. 1A, squares). However, deep colonies did not exhibit any afternoon depression under either light treatment, nor did the shallow colonies under full PAR light.

Temperature within the chambers was 22.0°C throughout the experiment, and this value was similar to the temperatures at 3 and 40 m during the time of the experiment (21.6 and 20.7°C, respectively).

Zooxanthellae densities, protein concentrations and chl *a* concentrations

Neither *Symbiodinium* density per surface area and biomass nor coral biomass, as measured by the mass of host protein per surface area,

Table 1. Gross photosynthesis to respiration (P_g/R), compensation light intensity (E_c) and efficiency of photosynthesis (apparent quantum yield, α) of shallow- and deep-water colonies of *Stylophora pistillata* under full-spectrum photosynthetically active radiation (PAR) and filtered blue light

Depth (m)	Light	P_g/R	E_c (μmol quanta m^{-2} s^{-1})	α
40	PAR	2.12	96.50±18.61	0.0002±0.0001
40	Blue	4.31	32.13±8.66	0.0003±0.0001
3	PAR	1.671	116.91±45.97	0.0011±0.0008
3	Blue	0.825	310.24±20.60	0.0002±0.0003

Data are means ± s.d. and are based on 24 h of oxygen and irradiance records (N=3).

significantly differed between corals from the 3 and 40 m depths (*t*-test, t_4=0.145, –2.019 and 1.717, respectively, P>0.05 for all, N=3). The mean zooxanthellae density per surface area was $1.46\times10^6\pm3.2\times10^5$ and $1.41\times10^6\pm6.0\times10^5$ cells cm^{-2} and the mean symbiont density per biomass was $1.54\times10^6\pm3.3\times10^5$ and $3.4\times10^6\pm2.2\times10^6$ cells mg^{-1} for the shallow and deep samples, respectively. The total protein content per surface area was 0.99±0.33 and 0.54±0.31 mg protein cm^{-2} in the shallow and deep colonies, respectively.

Chl *a* concentration per algal cell and per coral surface area was significantly different between the shallow and deep corals (*t*-test, t=2.12, P<0.05 in both cases, N=3). The chl *a* concentration per zooxanthellae was 1.78±0.67 and 5.78±0.86 pg chl *a* zooxanthellae^{-1} for the 3 and 40 m colonies, respectively, whereas the chl *a* concentration per surface area was 2.29±0.62 and 8.58±2.57 μg chl *a* cm^{-2}, respectively.

Coral absorption

Coral reflectivity results (Fig. 2) revealed a statistically significant difference ($F_{2,2170}$=2216, P<0.0001, N=10) in the absolute spectral reflectivity of corals collected from the two depth classes. The 3 m coral fragments reflected a significantly larger amount of irradiance than the 40 m sample, even at subsaturating light intensities. The 40 m corals displayed very low variability in reflection between 400 and 550 nm, indicating that a higher proportion of available light was being absorbed for photosynthesis compared with the 3 m corals. Second-order derivative analysis of the blue region of the reflected spectra revealed two additional absorption bands at 405 and 445 nm in the 40 m coral samples that were not present in the 3 m samples, most likely indicative of the higher chl *a* concentrations that were measured.

Aquatic irradiance measurements

The profile of the aquatic light in the Gulf of Aqaba during the experiment (3 April 2008) revealed that the euphotic zone occurred at a depth of 62 m with a PAR attenuation coefficient [$K_{d(PAR)}$] of 0.089 (Fig. 3). The $K_{d(PAR)}$ measured during this experiment was over an order of magnitude higher than the average value for the Gulf of Eilat of approximately 0.004, probably because of a high-wind-driven upwelling event and diatom bloom that occurred during the experimental period (Iluz et al., 2009). The light profiles shown were measured at noon and the other two profiles measured in the experimental period were similar and thus are not shown. The seasonal spectral irradiance profiles in the Gulf of Eilat are consistent, with differences in the morning and around sunset because of the angle of the sun (Stambler, 2008). The 490 nm channel had the lowest attenuation coefficient (K_d=0.056), with attenuation increasing towards the red region with a K_d of 0.449 at 665 nm. The ultraviolet range of the spectrum had attenuation rates slightly greater than those at 490 nm, but not as large as in the red channel, with a K_d of 0.077 at 395 nm. The light spectrum data (Fig. 4) suggest that, in shallow water (3 m), the spectrum available for photosynthesis is much wider than in deep water (40 m), with peak irradiance occurring at 465 nm and a gradual reduction towards both the red and ultraviolet range of the spectrum. In the deep-water (40 m) profile there was a significant narrowing of the available spectrum by the water column, with a shift in the peak irradiance received at depth further towards the blue region (490 nm) and steep reductions to either side of the peak. No light above 600 nm reached the bottom, creating a irradiance field dominated by blue light.

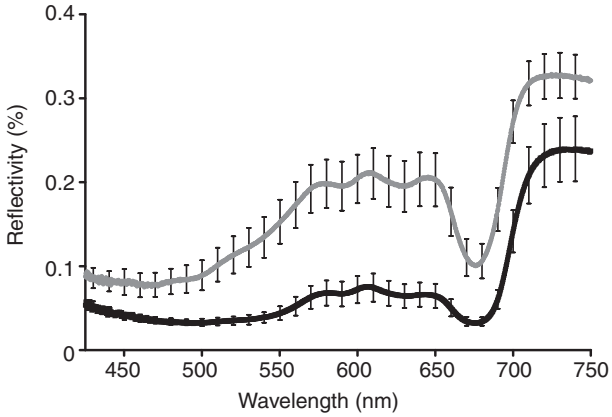

Fig. 2. *Stylophora pistillata* reflectivity *versus* wavelength (nm) for corals from 3 m (grey) and 40 m (black) depths. Error bars are ±s.d., marked every 10 nm.

DISCUSSION

This study reveals that shallow- and deep-water *S. pistillata* colonies exhibited a clear difference in their photosynthetic rates when exposed to full PAR *vs* blue light, presenting classical chromatic adaptation. Similar patterns of chromatic acclimation have been previously demonstrated in algae (Engelmann and Gaidukov, 1902), specifically with brown and red algae (Grossman, 2003) and in cyanobacteria (Dring, 1989; Schmid and Dring, 1996). Our results suggest that *Symbiodinium* spp., in a similar manner as plants and algae, use chromatic acclimation to optimize their light harvesting and utilization abilities in response to spatial and temporal changes in underwater irradiance (Falkowski and LaRoche, 1991).

There was a clear and significant relationship between colony depth and photosynthetic performance under blue light spectra. Deep corals showed higher photosynthetic performance when they were

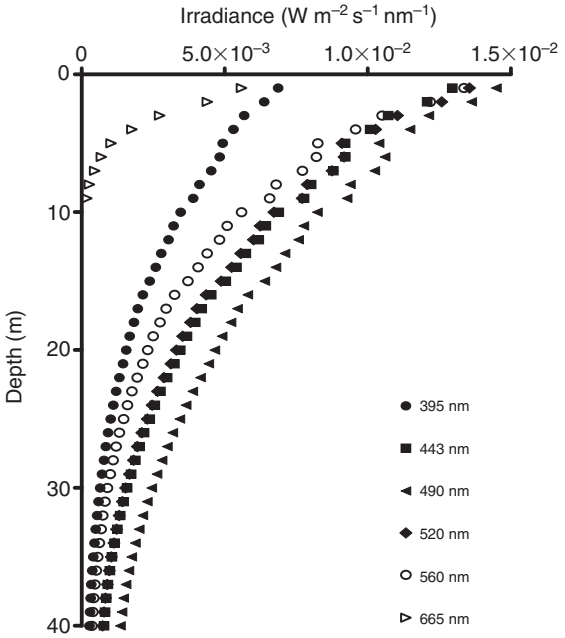

Fig. 3. Irradiance profiles (395–665 nm) collected from the waters adjacent to the Interuniversity Institute for Marine Sciences, Eilat, Israel, on 3 April 2008.

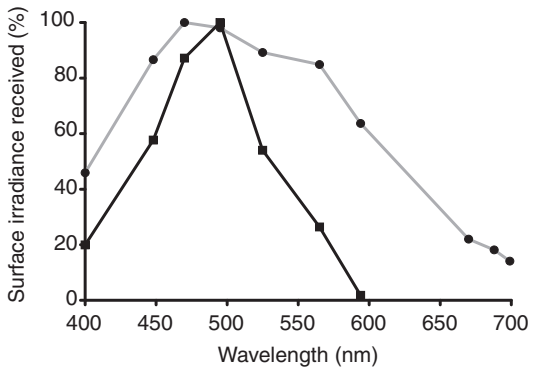

Fig. 4. Percent surface irradiance received of different wavelengths at 3 m (grey) and 40 m (black) depth in the waters adjacent to the Interuniversity Institute for Marine Sciences, Eilat, Israel, on 3 April 2008.

exposed to blue light in comparison to full PAR illumination under the same light intensities (Fig. 1B). The fact that corals were first exposed to PAR irradiance prior to being exposed to the blue light makes the results more conservative and strengthens the light spectrum photoacclimation phenomena. Shallow-water corals showed the opposite response, with higher photosynthetic performances under full-spectrum PAR than under the blue light (same irradiance, Fig. 1A). These results, along with the significant differences between the photosynthetic rates of the 3 and 40 m corals, reveal a clear biological signal, even with data from only three replicates. As the colonies were collected over 25 m away from each other, we assume that they are from different clones, and additional replicate corals or respirometer runs would have probably reinforced our findings.

Our underwater irradiance measurements from the Gulf of Aqaba during the experimental period provide light spectra for the two experimental collection depths (3 and 40 m) and reveal that the deep and shallow corals were exposed to strikingly different light spectra. As expected, deep corals were exposed to enriched blue light irradiance fields whereas the shallow corals had a much broader spectra of light available for photosynthesis. Although shallow-water corals are exposed to a full light spectrum, which includes blue, green and red wavelengths, deep colonies are predominantly exposed to blue wavelengths (Figs 3 and 4). The red component of the downwelling irradiance is strongly absorbed by the water molecules and by the chlorophyll of the phytoplankton. This attenuation, which is readily observed by divers, results in the steeper decrease in the red spectral range than in the range of total PAR, and, from a depth of approximately 10 m, their slopes increasingly diverge. Once the red component is filtered out, the remaining PAR consists mostly of the blue and green spectral components and its attenuation parallels that of the 412 nm band (Siegel and Dicky, 1987; Platt and Sathyendranath, 1988). At a depth of 3 m, the ratio of blue and green spectral components to PAR is lower than at 40 m, but the ratio of the red component to PAR is considerably higher (Fig. 3). Indeed, the value (red/PAR)/(blue+green/PAR) at 3 m is 0.351 and decreases at 40 m to as low as 0.009. The response of the coral colonies to these spectral differences was evident in the absorbance spectrum of the corals, with the shallow corals reflecting a significantly higher proportion of the light spectrum than the deep corals and the deep corals absorbing a higher proportion of the blue light (Fig. 2). Kinzie et al. showed that the coral–algal symbiotic system and zooxanthellae cultures showed different growth responses to light of differing spectral composition (Kinzie et al., 1984). In particular, corals grown under blue or white light showed increased growth and had higher algal densities than corals grown in green or red light. These authors suggested that the blue-light response represented a physiological adaptation to provide higher photosynthetic efficiency with increasing depth in the field (Kinzie et al., 1984).

The principal mechanism that *S. pistillata* colonies growing in Eilat use to photoacclimate to increasing depth is to increase their chlorophyll content without changing their zooxanthellae numbers (Falkowski and Dubinsky, 1981; Mass et al., 2007; Winters et al., 2009). Dinoflagellates in general and zooxanthellae in particular (Dubinsky and Jokiel, 1994) display an increased chl *a* concentration per cell in the process of acclimation to low-light intensity (Falkowski and Dubinsky, 1981; Dubinsky et al., 1984), a universal response also found in free-living phytoplankton (Dubinsky et al., 1986). However, studies from other reef locations have found that zooxanthellae numbers can increase when corals are grown at increasing depths (Dustan, 1982; Titylanov et al., 2001) suggesting that photoacclimation mechanisms to increasing depth for different coral species or the same species growing in different environments may vary (Winters et al., 2009). Furthermore, histological studies on *S. pistillata* colonies from Eilat have revealed that the zooxanthellae of shallow colonies growing in high light exhibited morphological photoacclimation, resulting in smaller zooxanthellae (Titylanov et al., 2001; Winters et al., 2009) that grew deeper inside the host tissue compared with deeper colonies (Winters et al., 2009). The smaller zooxanthellae found at high light could have resulted from more rapid division and degradation rates of the algae resulting from increasing damage at high light, leading to a population of smaller, younger zooxanthellae (Dustan, 1982; Titylanov et al., 2001). Conversely, larger zooxanthellae reported from colonies at depth may result from slower rates of division and degradation, with lower light levels leading to older, larger zooxanthellae populations (Titylanov et al., 2000; Titylanov et al., 2001). Our results support the classical photoacclimation mechanism as proposed by Falkowski and Dubinsky (Falkowski and Dubinsky, 1981), showing an increase in chl *a* concentrations with depth.

The increase in chl *a* concentration in the deep corals from the present study without a concomitant change in zooxanthellae numbers may result in increased overlap between the optical cross-sections of the thylakoid stacks and, potentially, self-shading by these pigment molecules or a ‘packaging effect’ (Kirk, 1994; Geider and Osborne, 1987; Stambler and Dubinsky, 2005). Wyman et al. found that the self-shading of thylakoid stacks in deep corals is overwhelmed by the increased portion of light that is useable for photosynthesis at depth because of the changing spectral quality of the light (Wyman et al., 1987). Furthermore, Stambler and Dubinsky reported that the self-shading by chlorophyll pigments at high chlorophyll concentrations may decrease the percent absorption per chlorophyll but the higher chlorophyll concentrations will always increase the total light absorption (Stambler and Dubinsky, 2005).

Additional support for the classic photoacclimation mechanism was suggested by the two additional chl *a* absorption bands we found at 405 and 445 nm in the 40 m corals (Fig. 2) (Jeffrey and Haxo, 1968), as the spectral reflectance properties of phototropic corals are intrinsically linked to the amount of pigments in the zooxanthellae (Hochberg et al., 2006). The increase in photosynthetic pigments reported here and the spectral absorption properties of the antenna complexes present in the deep-water corals (Fig. 2) may explain the difference in the coral reflectance curves. Additionally, the spectral reflectance data presented in this paper for *S. pistillata* conforms to other studies conducted both in the Red Sea (Minghelli-Roman et al.,

2002; Wettle et al., 2003) and from 11 sites around the world (Hochberg et al., 2003; Lesser et al., 2010). In these previously published studies there was very little light reflected from the surface of corals, as the majority was absorbed by the zooxanthellae. Furthermore, a difference in the *Symbiodinium* clades between the shallow- and deep-water colonies of *S. pistillata* from Eilat has been previously reported (Winter et al., 2009). Colonies from shallow water have been shown to possess clade A whereas deep-water *S. pistillata* colonies (>30 m) possess clade C (Karako-Lampert et al., 2004; Winters et al., 2009). Studies in the Caribbean have found that other corals that are found along a broad depth gradient switch from hosting clade A or B zooxanthellae in shallow water to clade C in deeper water, possibly owing to the ability of the different clades to adapt to different light levels (Rowan and Knowlton, 1995; Baker et al., 1997). Winters et al. have also suggested that the difference in clades found in *S. pistillata* colonies from different depths could be due to the thermal tolerances of the zooxanthellae clades, and they present data suggesting that corals hosting clade C symbionts are less thermally tolerant than those hosting clade A (Winters et al., 2009). The difference in zooxanthellae clades could also contribute to the adaptation of *S. pistillata* corals to the deep, blue light environment. However, further research is required to fully examine the chromatic acclimation adaptation of different clades to different light regimes, which was not the scope of the present study.

Deep corals growing under the maximum daily light intensity had approximately 30% higher oxygen production than the shallow corals (Fig. 1). In this study, however, there were differences in maximum light intensities between the days when the experiments were run, with the deep corals run at a maximum light intensity of $500\,\mu mol\,m^{-2}\,s^{-1}$ and the shallow corals run at a maximum light intensity of only $400\,\mu mol\,m^{-2}\,s^{-1}$. These differences in maximum light intensities could have accounted for the difference in oxygen production. Alternatively, the higher oxygen production of the deep corals could also imply that corals could adapt to the transplantation from shallow to deep depths more easily than from deep to shallow. The greater oxygen accumulation of the deep corals could lead to photoinhibition, owing to the high photon flux damaging photosystem II, and to the accumulation of reactive oxygen species that could damage the chloroplasts (Finelli et al., 2006; Lesser et al., 1994). This suggests that the photoadaptation for reduced light in our study could be more efficient than the adaptation mechanism to higher light levels, as has been found in a previous study (Anthony and Hoegh-Guldberg, 2003). Furthermore, in many previous studies (Dustan, 1982; Yap et al., 1998; Baker, 2001), corals transplanted from deep to shallow depths probably died from ultraviolet irradiance exposure or photodamage, providing further evidence that corals have a harder time adapting after transplantation to higher light levels.

When the shallow corals were exposed to blue light on the second day of the experiment, they showed a delay in oxygen production, causing a reverse hysteresis pattern with oxygen rates higher in the afternoon compared with the morning for the same light intensity (Fig. 1A) (Levy et al., 2004). This finding is contradictory to those studies reporting an 'afternoon nap' or a decrease in afternoon photosynthetic rates (Schanz and Dubinsky, 1988; Vollenweider, 1965; Vollenweider and Nauwerck, 1961). The fact that corals from 3 m depth did not show hysteresis under full-spectrum PAR differs from the results of Levy et al. (Levy et al., 2004) and may be a seasonal effect – our measurements occurred during the spring months of March–April whereas the work in 2004 was based on measurements taken during the summer months of June–August. Although still an assumption, the evidence from this work and earlier studies (Levy et al., 2004; Mass et al., 2007) indicates that the reverse hysteresis phenomenon is associated with daily, monthly and annual cycles and is probably related to the core circadian clock machinery (Harmer et al., 2000).

The present study clearly demonstrates the chromatic adaptation of *S. pistillata* to its light environment by presenting physiological evidence of changes in photosynthetic performance under different light spectrum. The corals from shallow water are clearly adapted to full light spectra whereas deep corals are adapted to blue light spectra. Thus, chromatic adaptation and, probably, the zooxanthellae cladal differences provide selective advantages by maximizing photon capture and photosynthetic activity under the different spectral conditions that occur in the reefs of Eilat, Red Sea.

LIST OF ABBREVIATIONS

chl *a*	chlorophyll *a*
E_c	compensation light levels
EPIR	enhanced post-illumination respiration
K_d	diffuse attenuation coefficient
$K_{d(PAR)}$	PAR attenuation coefficient
P	photosynthesis
PAR	photosynthetically active radiation
P_g/R	ratio of gross photosynthesis to respiration
P_{max}	maximal photosynthesis rate
R	respiration
α	initial slope of photosynthesis *vs* irradiance curves

ACKNOWLEDGEMENTS

This study was performed during the 8th International Workshop of Group for Aquatic Primary Productivity (GAP) and Batsheva de Rothschild Seminar on Gross and Net Primary Productivity held at the Interuniversity Institute for Marine Sciences, Eilat, Israel, in April 2008. We thank the Batsheva de Rothschild Foundation, Bar Ilan University, the Moshe Shilo Center for Marine Biogeochemistry, the Nato SfP Foundation and the staff of the Interuniversity Institute for funding and logistic support. This research was also supported by Australian Research Council grants to the Ove Hoegh-Guldberg Coral Reef Ecosystems lab. This manuscript was significantly improved based on the suggestions of two anonymous reviewers.

REFERENCES

Alieva, N. O., Konzen, K. A., Field, S. F., Meleshkevitch, E. A., Hunt, M. E., Beltran-Ramirez, V., Miller, D. J., Wiedenmann, J., Salih, A. and Matz, M. V. (2008). Diversity and evolution of coral fluorescent proteins. *PLoS ONE* **3**, e2680.

Anthony, K. R. N. and Hoegh-Guldberg, O. (2003). Variation in coral photosynthesis, respiration and growth characteristics in contrasting light microhabitats: an analogue to plants in forest gaps and understoreys? *Funct. Ecol.* **17**, 246-259.

Baker, A. C. (2001). Reef corals bleach to survive change. *Nature* **411**, 765–766.

Baker, A. C., Rowan, R. and Knowlton, N. (1997). Symbiosis ecology of two Caribbean acroporid corals. *Proc. 8th Int. Coral Reef Symp. Panama* **2**, 1295-1300.

Beardall, J., Burger-Wiersma, T., Rykeboer, M., Sukenik, A., Lemoalle, J., Dubinsky, Z. and Fontvielle, D. (1994). Studies on enhanced post-illumination respiration in microalgae. *J. Plankton Res.* **16**, 1401-1410.

Benzion, M. and Dubinsky, Z. (1988). An online system for measuring photosynthetic characteristics via an oxygen electrode. *J. Plankton Res.* **10**, 555-558.

Bradford, M. M. (1976). Rapid and sensitive method for quantitation of microgram quantities of protein utilizing principle of protein-dye binding. *Anal. Biochem.* **72**, 248-254.

Carpenter, J. H. (1965). The Chesapeake Bay Institute technique for the Winkler dissolved oxygen titration. *Limnol. Oceanogr.* **10**, 141-143.

Crossland, C. J., Hatcher, B. G. and Smith, S. V. (1991). Role of coral reefs in global ocean production. *Coral Reefs* **10**, 55-64.

D'Angelo, C., Denzel, A., Vogt, A., Matz, M. V., Oswald, F., Salih, A., Nienhaus, G. U. and Wiedenmann, J. (2008). Blue light regulation of host pigment in reef-building corals. *Mar. Ecol. Prog. Ser.* **364**, 97-106.

Dring, M. J. (1989). Stimulation of light-saturated photosynthesis in *Laminaria* (Phaeophyta) by blue light. *J. Phycol.* **25**, 254-258.

Dubinsky, Z. and Jokiel, P. (1994). The ratio of energy and nutrient fluxes regulates the symbiosis between zooxanthellae and corals. *Pac. Sci.* **48**, 313-324.

Dubinsky, Z., Falkowski, P. G., Porter, J. W. and Muscatine, L. (1984). Absorption and utilization of radiant energy by light- and shade-adapted colonies of the hermatypic coral *Stylophora pistillata*. *Proc. R. Soc. Lond. B Biol. Sci.* **222**, 203-214.

Dubinsky, Z., Falkowski, P. G. and Wyman, K. (1986). Light harvesting and utilization in phytoplankton. *Plant Cell Physiol.* **27**, 1335-1349.

Dustan, P. (1982). Depth-dependent photoadaption by zooxanthellae of the reef coral *Montastrea annularis*. *Mar. Biol.* **68**, 253-264.

Einbinder, S., Mass, T., Brokovich, E., Dubinsky, Z., Erez, J. and Tchernov D. (2009). Changes in morphology and diet of the cora*l Stylophora pistillata* along the depth gradient. *Mar. Ecol. Prog. Ser.* **381**, 167-174.

Engelmann, T. W. and Gaidukov, N. I. (1902). Ueber experimentelle Erzeugung zweckmassiger Aenderungen der Farbung pflanzlicher Chromophylle durch farbiges Licht. *Arch. Anat. Physiol. Physiol. Abt.* 333-335.
Enriquez, S., Mendez, E. R. and Iglesias-Prieto, R. (2005). Multiple scattering on coral skeletons enhances light absorption by symbiotic algae. *Limnol. Oceanogr.* **50**, 1025-1032.
Esper, E. J. C. (1797). Fortsetzungen der Pflanzenthiere in Abbildungen nach der Natur mit Farben erleuchtet nebst Beschreibungen. *Erster Theil. (Nürnberg).* 230 pp.
Fabricius, K. E. and Klumpp, D. W. (1995). Widespread mixotrophy in reef-inhabiting soft corals: the influence of depth, and colony expansion and contraction on photosynthesis. *Mar. Ecol. Prog. Ser.* **125**, 195-204.
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.
Falkowski, P. G. and LaRoche, J. (1991). Acclimation to spectral irradiance in algae. *J. Phycol.* **27**, 8-14.
Falkowski, P. G., Dubinsky, Z., Muscatine, L. and Porter, J. W. (1984). Light and the bioenergetics of a symbiotic coral. *BioScience* **34**, 705-709.
Falkowski, P. G., Dubinsky, Z. and Santostefano. G. (1985). Light-enhanced dark respiration in phytoplankton. *Verh. Int. Verein. Limnol.* **22**, 2830-2833.
Falkowski, P. G., Jokeil, P. L. and Kinsie, R. A. (1990). Irradiance and corals. In *Ecosystems of the World: Coral Reefs* (ed. Z. Dubinsky), pp. 89-106. New York: Elsevier Press.
Finelli, C. M., Helmuth, B. S. T., Pentcheff, N. D. and Wethey, D. S. (2006). Water flow influences oxygen transport and photosynthetic efficiency in corals. *Coral Reefs* **25**, 47-57.
Geider, R. J. and Osborne, B. A. (1987). Light absorption by a marine diatom: experimental observation and theoretical calculations of the package effect in a small *Thalassiosira* species. *Mar. Biol.* **96**, 299-308.
Genin, A., Monismith, S. G., Reidenbach, M. A., Yahel, G. and Koseff, J. R. (2009). Intense benthic grazing of phytoplankton in a coral reef. *Limnol. Oceanogr.* **54**, 938-951.
Glynn, P. (1996). Coral reef bleaching: facts, hypotheses and implications. *Global Change Biol.* **2**, 495-509.
Gordon, H. R. (1989). Can the Lambert-Beer law be applied to the diffuse attenuation coefficient of ocean water? *Limnol. Oceanogr.* **34**, 1389-1409.
Grossman, A. R. (2003). A molecular understanding of complementary chromatic adaptation. *Photosynth. Res.* **76**, 207-215.
Harmer, S. L., Hogenesch, J. B., Straume, M., Chang, H. S., Han, B., Zhu, T., Wang, X., Kreps, J. A. and Kay, S. A. (2000). Orchestrated transcription of key pathways in arabidopsis by the circadian clock. *Science* **290**, 2110-2113.
Hochberg, E. J., Atkinson, M. J. and Andréfouët, S. (2003). Spectral reflectance of coral reef bottom-types worldwide and implications for coral reef remote sensing. *Remote Sens. Environ.* **85**, 159-173.
Hochberg, E. J., Apprill, A. M., Atkinson, M. J. and Bidigare, R. R. (2006). Bio-optical modeling of photosynthetic pigments in corals. *Coral Reefs* **25**, 99-109.
Hoegh-Guldberg, O. (1999). Climate change, coral bleaching and the future of the world's coral reefs. *Mar. Freshw. Res.* **50**, 839-866.
Houlbrèque, F., Delesalle, B., Blanchot, J., Montel, Y. and Ferrier-Pagès, C. (2006). Picoplankton removal by the coral reef community of La Prévoyante, Mayotte Island. *Aquat. Microb. Ecol.* **44**, 59-70.
Hughes, T. P., Baird, A. H., Bellwood, D. R., Card, M., Connolly, S. R., Folke, C., Grosberg, R., Hoegh-Guldberg, O., Jackson, J. B. C., Kleypas, J. et al. (2003). Climate change, human impacts, and the resilience of coral reefs. *Science* **301**, 929-933.
Iluz, D. (1998). The light field, phytoplankton pigmentation and productivity in the Gulf of Eilat (Hebrew with English abstract). Red Sea. DIALOG III; Dissertations Initiative for the Advancement of Limnology and Oceanography, pp. 86-88.
Iluz, D., Yacobi, Y. Z. and Gitelson, A. (2003). Adaptation of an algorithm for chlorophyll-a estimation by optical data in the oligotrophic Gulf of Eilat. *Int. J. Remote Sens.* **24**, 1157-1163.
Iluz, D., Dishon, G., Capuzzo, E., Meeder, E., Astoreca, R., Montecino, V., Znachor, P., Ediger, D. and Marra, J. (2009). Short-term variability in primary productivity during a wind-driven diatom bloom in the Gulf of Eilat (Aqaba). *Aquat. Microb. Ecol.* **56**, 205-215.
Jeffrey, S. W. and Haxo, F. T. (1968). Photosynthetic pigments of symbiotic dinoflagellates (zooxanthellae) from corals and clams. *Biol. Bull.* **135**, 149-165.
Jeffrey, S. W. and Humphrey, G. F. (1975). New spectrophotometric equations for determining chlorophylls a, b, c1, and c2 in higher plants, algae and natural phytoplankton. *Biochem. Physiol. Pflanzn.* **167**, 191-194.
Jerlov, N. G. (1968). *Optical Oceanography*. Amsterdam: Elsevier Publishing Company.
Jerlov, N. G. (1976). *Marine Optics (Elsevier Oceanography Series)*, Vol. 14. Amsterdam: Elsevier Scientific Publishers.
Karako-Lampert, S., Katcoff, D. J., Achituv, Y., Dubinsky, Z. and Stambler, N. (2004). Do clades of symbiotic dinoflagellates in scleractinian corals of the Gulf of Eilat (Red Sea) differ from those of other coral reefs? *J. Exp. Mar. Biol. Ecol.* **311**, 301-314.
Kinzie, R. A., Jokiel, P. L. and York, R. (1984). Effects of light of altered spectral composition on coral zooxanthellae associations and on zooxanthellae in vitro. *Mar. Biol.* **78**, 239-248.
Kirk, J. T. O. (1994). *Light and Photosynthesis in Aquatic Ecosystems*, 2nd edn. London: Cambridge University Press.
Lesser, M. P., Weis, V. M., Patterson, M. R. and Jokiel, P. L. (1994). Effects of morphology and water motion on carbon delivery and productivity in the reef coral, *Pocillopora damicornis* (Linnaeus): diffusion barriers, inorganic carbon limitation, and biochemical plasticity. *J. Exp. Mar. Biol. Ecol.* **178**, 153-179.
Lesser, M. P., Slattery, M., Stat, M., Ojimi, M., Gates, R. D. and Grottoli, A. (2010). Photoacclimatization by the coral *Montastraea cavernosa* in the mesophotic zone: light, food, and genetics. *Ecology* **91**, 990-1003.
Levy, O., Dubinsky, Z., Schneider, K., Achituv, Y., Zakai, D. and Gorbunov, M. Y. (2004). Diurnal hysteresis in coral photosynthesis. *Mar. Ecol. Prog. Ser.* **268**, 105-117.
Levy, O., Appelbaum, L., Leggat, W., Gothlif, Y., Hayward, D. C., Miller, D. J. and Hoegh-Guldberg, O. (2007). Light-responsive cryptochromes from a simple multicellular animal, the coral *Acropora millepora*. *Science* **318**, 467-470.
Loya, Y. (1976). The Red Sea coral *Stylophora pistillata* is an r strategist. *Nature* **259**, 478-480.
Mass, T., Einbinder, S., Brokovich, E., Shashar, N., Vago, R., Erez, J. and Dubinsky, Z. (2007). Photoacclimation of *Stylophora pistillata* to light extremes: metabolism and calcification. *Mar. Ecol. Prog. Ser.* **334**, 93-102.
Minghelli-Roman, A., Chisholm, J. R. M., Marchioretti, M. and Jaunert, J. M. (2002). Discrimination of coral reflectance spectra in the Red Sea. *Coral Reefs* **21**, 307-314.
Morel, A. and Prieur, L. (1977). Analysis of variations in ocean color. *Limnol. Oceanogr.* **22**, 709-722.
Muscatine, L. (1990). The role of symbiotic algae in carbon and energy flux in reef corals. In *Ecosystems of the World: Coral Reefs* (ed. Z. Dubinsky), pp. 75-87. New York: Elsevier Press.
Platt, T. and Sathyendranath, S. (1988). Oceanic primary production: estimation by remote sensing at local and regional scales. *Science* **241**, 1613-1620.
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. R. Soc. Lond. B Biol. Sci.* **222**, 161-180.
Rowan, R. and Knowlton, N. (1995). Intraspecific diversity and ecological zonation in coral algal symbiosis. *Proc. Natl. Acad. Sci. USA* **92**, 2850-2853.
Schanz, F. and Dubinsky, Z. (1988). The afternoon depression in primary productivity in a high rate oxidation pond (HROP). *J. Plankton Res.* **10**, 373-383.
Schmid, R. and Dring, M. J. (1996). Influence of carbon supply on circadian rhythmicity of photosynthesis and its stimulation by blue light in *Ectocarpus siliculosus*: clues to the mechanism of inorganic carbon acquisition in lower brown algae. *Plant Cell Environ.* **19**, 373-382.
Schuhmacher, H. and Zibrowius, H. (1985). What is hermatypic? A redefinition of ecological groups in corals and other organisms. *Coral Reefs* **4**, 1-9.
Siegel, D. A. and Dickey, T. D. (1987). Observations of the vertical structure of the diffuse attenuation coefficient spectrum. *Deep-Sea Res.* **34**, 547-563.
Smith, R. C. and Baker, K. S. (1981). Optical properties of the clearest natural waters (200–800 nm). *Appl. Opt.* **20**, 177-184.
Stambler, N. (1998). Effects of light intensity and ammonium enrichment on the hermatypic coral *Stylophora pistillata* and its zooxanthellae. *Symbiosis* **24**, 127-146.
Stambler, N. (2006). Light and picophytoplankton in the Gulf of Eilat (Aqaba). *J. Geophys. Res.* **111**, C11009.
Stambler, N. (2008). Light, pico-phytoplankton and coral in the blue waters of the Gulf of Eilat. In *Aqaba-Eilat, the Improbable Gulf. Environment, Biodiversity and Preservation* (ed. F. D. Por), pp. 63-74. Jerusalem: Magnes Press.
Stambler, N. and Dubinsky, Z. (2005). Corals as light collectors: an integrating sphere approach. *Coral Reefs* **24**, 1-9.
Stimson, J. and Kinzie, R. A., III (1991). The temporal pattern and rate of release of zooxanthellae from the reef coral *Pocillopora damicornis* (Linnaeus) under nitrogen-enrichment and control conditions. *J. Exp. Mar. Biol. Ecol.* **153**, 63-74.
Titlyanov, E. A. (1991). Light adaptation and production characteristics of branches differing by age and illumination of the hermatypic coral *Pocillopora verrucosa*. *Symbiosis* **10**, 249-260.
Titlyanov, E. A., Bil', K., Fomina, I., Titlyanova, T. V., Leletkin, V., Eden, N., Malkin, A. and Dubinsky, Z. (2000). Effects of dissolved ammonium addition and host feeding with *Artemia salina* on photo-acclimation of the hermatypic coral *Stylophora pistillata*. *Mar. Biol.* **137**, 463-472.
Titlyanov, E. A., Titlyanova, T. V., Yamazato, K. and Van Woesik, R. (2001). Photo-acclimation dynamics of the coral *Stylophora pistillata* to low and extremely low light. *J. Exp. Mar. Biol. Ecol.* **263**, 211-225.
Vollenweider, R. A. (1965). Calculative models of photosynthesis-depth curves and some implications regarding day rate estimates in primary production measurements. *Mem. Ist. Ital. Idrobiol.* **18**, 425-457.
Vollenweider, R. A. and Nauwerck, A. (1961). Some observations on the C^{14} method for measuring primary production. *Verh. Internat. Verein. Limnol.* **14**, 134-139.
Wells, J. W. (1957). Corals. *Mem. Geol. Soc. Am.* **67**, 1087-1104.
Wettle, M., Ferrier, G., Lawrence, A. J. and Anderson, K. (2003). Fourth order derivatives analysis of Red Sea coral reflectance spectra. *Int. J. Remote Sens.* **24**, 3867-3872.
Winkler, L. W. (1888). Die Bestimmung des in Wasser gelösten Sauerstoffen. *Ber. Deutsch Chem. Gos.* **21**, 2843-2855.
Winters, G., Beer, S., Zvi, B. B., Brickner, I. and Loya, Y. (2009). Spatial and temporal photoacclimation of *Stylophora pistillata*: zooxanthella size, pigmentation, location and clade. *Mar. Ecol. Prog. Ser.* **384**, 107-119.
Wyman, K. D., Dubinsky, Z., Porter, J. W. and Falkowski, P. G. (1987). Light absorption and utilization among hermatypic corals: a study in Jamaica, West Indies. *Mar. Biol.* **96**, 283-292.
Yahel, G., Post, A. F., Fabricius, K., Marie, D., Vaulot, D. and Genin, A. (1998). Phytoplankton distribution and grazing near coral reefs. *Limnol. Oceanogr.* **43**, 551-563.
Yap, H. T., Alvarez, R. M., Custodio, H. M. III and Dizon, R. M. (1998). Physiological and ecological aspects of coral transplantation. *J. Exp. Mar. Biol. Ecol.* **229**, 69-84.
Yentsch, C. S., Yentsch, C. M., Cullen, J. J., Lapointe, B., Phinney, D. A. and Yentsch, S. W. (2002). Sunlight and water transparency: cornerstones in coral research. *J. Exp. Mar. Biol. Ecol.* **268**, 171.