The Journal of Experimental Biology 213, 4304-4312

doi:10.1242/jeb.044941

Shallow-water wave lensing in coral reefs: a physical and biological case study

Cameron James Veal[1,2,*], Maya Carmi[2], Gal Dishon[2], Yoni Sharon[2], Kelvin Michael[3], Dan Tchernov[2,4,5], Ove Hoegh-Guldberg[1] and Maoz Fine[2,6]

[1]Global Change Institute, Coral Reef Ecosystem Laboratory, The University of Queensland, St Lucia, Brisbane, Queensland 4072, Australia, [2]The Interuniversity Institute for Marine Science, Eilat 88103, Israel, [3]Institute for Marine and Antarctic Studies, University of Tasmania, Sandy Bay, Tasmania 7001, Australia, [4]The Alexander Silberman Institute of Life Sciences, The Hebrew University of Jerusalem, Jerusalem 91904, Israel, [5]Marine Biology Department, The Leon H. Charney School of Marine Sciences, University of Haifa, Mount Carmel, Haifa 31905, Israel and [6]The Mina and Everard Goodman Faculty of Life Science, Bar-Ilan University, Ramat Gan 52900, Israel

*Author for correspondence (c.veal@uq.edu.au)

Accepted 25 September 2010

SUMMARY

Wave lensing produces the highest level of transient solar irradiances found in nature, ranging in intensity over several orders of magnitude in just a few tens of milliseconds. Shallow coral reefs can be exposed to wave lensing during light-wind, clear-sky conditions, which have been implicated as a secondary cause of mass coral bleaching through light stress. Management strategies to protect small areas of high-value reef from wave-lensed light stress were tested using seawater irrigation sprinklers to negate wave lensing by breaking up the water surface. A series of field and tank experiments investigated the physical and photophysiological response of the shallow-water species *Stylophora pistillata* and *Favites abdita* to wave lensing and sprinkler conditions. Results show that the sprinkler treatment only slightly reduces the total downwelling photosynthetically active and ultraviolet irradiance (~5.0%), whereas it dramatically reduces, by 460%, the irradiance variability caused by wave lensing. Despite this large reduction in variability and modest reduction in downwelling irradiance, there was no detectable difference in photophysiological response of the corals between control and sprinkler treatments under two thermal regimes of ambient (27°C) and heated treatment (31°C). This study suggests that shallow-water coral species are not negatively affected by the strong flashes that occur under wave-lensing conditions.

Key words: coral, wave lensing, light.

INTRODUCTION

Shallow-water marine ecosystems are one of the most biologically productive regions on Earth (Ackelson, 2003), and light is the predominant resource for which phototrophic organisms compete by building complex three-dimensional structures, ultimately designed for light acquisition. The spatial complexity resulting from the structure of aquatic canopies, coupled with environmental variability, causes significant seasonal, diurnal and spatial variability in downwelling irradiance levels (Veal et al., 2009).

Downwelling irradiance is the most variable physical parameter in the oceans of the world. It varies in intensity on the scales of years to milliseconds (Stramski and Legendre, 1992). Over fractions of seconds, fluctuations in downwelling irradiance are driven by alternating focusing and defocusing of bundles of refracted sun rays as they cross the curved surfaces of waves, reaching down to depths of 35 m (Stramski and Legendre, 1992; Stramska and Dickey, 1998). Convex sections of waves act as a converging lens, focusing the light at various depths, dependent on the slope of the wave and the incidence angle of the light (Kirk, 1994). These focused light fields, also known as 'underwater light flashes' or light caustics, are defined as a pulse of underwater downwelling irradiance that is at least 150% of the average downwelling irradiance at that depth (Stramski, 1986). The lensed component of light comprises solely unscattered or forward-scatted radiation, with the intensity of the flash being constant under varying sky conditions, provided that this directional component of surface irradiance is >50% (Stramski, 1986; Stramski and Dera, 1988). The flash duration lasts from 10 to 300 ms, with intensity varying up to six times the mean downwelling irradiance under ideal conditions in the visible spectrum (Stramski and Dera, 1988). Wave-lensing conditions occur under light winds (2–7 $m\,s^{-1}$), when small capillary or gravitational waves of up to 20 cm in amplitude form sheets of waves extending in a direction perpendicular to that of the wind (Weidemann et al., 1990; Stramski and Legendre, 1992; Cepic, 2008). Waves occur along the phase boundary of an aqueous medium where fluid dynamics are controlled by surface tension. Under these wave conditions, it might be possible to produce >350 light flashes every minute at a depth of 1 m (Weidemann et al., 1990), with a single flash capable of exceeding an intensity of 9000 $\mu mol\ quanta\ m^{-2}\,s^{-1}$ in extremely shallow waters (Shubert et al., 2001).

Ecophysiological studies involving the effects of irradiance on organisms cannot correctly characterise the response of an organism without an accurate assessment of the irradiance climate (Shubert et al., 2001). Despite extensive documentation of the optical properties of shallow waters (Jerlov, 1976; Stramska and Dickey, 1998; Kirk, 1994) and knowledge of wave lensing for the past 50 years (Schenck, 1957), our understanding of organism function and aquatic photosynthesis under fluctuating illumination, both qualitatively (light spectrum) and quantitatively, is still very limited (Rascher and Nedbal, 2002; Shubert et al., 2001).

It is well documented that the photosynthetic rate of an organism depends not only on the amount of irradiance received but the manner in which it is delivered (Stramska and Dickey, 1998). There has been a handful of studies investigating the effect of flashing or fluctuating light on marine phytoplankton and macroalgae (Walsh and Legrendre, 1983; Greene and Gerard, 1990; Grobbelaar et al., 1996). Research into marine phytoplankton cultures has found that flashing light can increase photosynthetic yield and carbon assimilation in some optically dense media (Queginer and Legendre, 1986) yet reduce them in others (Stramski et al., 1993). Studies on three macroalgae (*Hormosira banksii*, *Carpophyllum maschalocarpum* and *Ecklonia radiata*) found increased photosynthesis under fluctuating light, provided that the light levels were between suboptimal and saturating; fluctuations above saturating levels did not increase photosynthetic efficiency (Dromgoole, 1988). Research on *Palmaria palmata* recorded reduced growth under fluctuating light due to reduced carbon uptake, whereas *Lomentaria articulata* was unaffected by dynamic or static light fields (Kübler and Raven, 1996). Beer and colleagues reported variable photosynthetic yields collected from seagrass in the Gulf of Eilat due to wave lensing (Beer et al., 1998). Nakamura and Yamaski investigated the influence of fluctuating light on *Acropora digitifera* (Nakamura and Yamaski, 2008); however, with only six light flashes per minute, and an intensity of 500 μmol quanta m^{-2} s^{-1}, the results do not realistically depict a shallow-water coral reef light environment, where both irradiance and flash frequency are several orders of magnitude greater.

High levels of solar irradiance have long been suspected to contribute to coral bleaching (Dunne and Brown, 1996; Hoegh-Guldberg, 1999; Winters et al., 2009). The increased frequency of bleaching events and impaired recovery of reefs post-bleaching require the development of management strategies to increase reef resilience and reduce climatic pressures on the reefs (Bruno and Selig, 2007; Hoegh-Guldberg et al., 2007). One method proposed to protect small regions of high-value reef from solar-irradiance-induced bleaching was the use of small in-water shade cloths suspended above shallow coral regions (E. Ström, unpublished); however, this had significant shortcomings owing to marine fouling, manual handling and drowning risk to snorkelers caused by the overhead environment in high-use coral reefs (e.g. when adjacent to tourism pontoons).

In an attempt to circumvent some of these limitations, we proposed to investigate whether an irrigation unit could be used to spray droplets of salt water over several tens of metres of shallow-water reef. The water droplets were hypothesised to dampen the high light-variability caused by wave lensing and possibly reduce photosynthetic stress on shallow-water corals during wind conditions that favour wave lensing. To test this hypothesis, it was essential to understand the physics of wave lensing and the sprinklers, as well as the biological response of the photosynthetic apparatus of the corals to the modified light-field dynamics.

MATERIALS AND METHODS

Study site

This study was conducted between June and August 2009 in the waters and coral reef adjacent to the Interuniversity Institute for Marine Science (IUI), near Eilat at the northern tip of the Gulf of Eilat (Aqaba), Red Sea (29°30′ N, 34°55′ E), Israel.

Wave-lensing irradiance measurements

Spectral measurements of downwelling irradiance along the coral reef slope of the waters adjacent to the IUI were measured with a PRR800 high-resolution profiling reflectance radiometer (Biospherical Instruments, San Diego, CA, USA). This 2π SeaWiFS-compliant reference radiometer, with 19 channels in the ultraviolet and visible range of the spectrum, is capable of measuring at 15 Hz with an integration time of 50 ms. The radiometer was connected to a surface deckbox and power supply that relayed information to a laptop computer. The PRR800 was deployed using the aquatic calibration model by SCUBA divers to depths ranging from 2 to 30 m at solar noon on 5 and 6 July 2009 under conditions of light winds and clear sky. The unit was placed on the reef slope and levelled at each depth, with the divers then swimming 20 m away from the sensor to prevent exhaust gas bubbles changing the light field. Measurements were conducted for several minutes at each depth, before the sensor was returned to the surface to collect surface irradiance and dark calibration values. Aquatic measurements were surface normalised using the average surface irradiance for the 20 min sample period, collected with the PRR800 using the surface calibration mode. Continuous surface radiation measurements were also made using a CB11B global pyranometer (Kipp and Zonen, Delftechpark, The Netherlands) operated as part of the Israel National Monitoring Program at the Gulf of Eilat weather station located on the IUI Pier (http://www.iui-eilat.ac.il/NMP/). The PRR800 data were then extracted to determine the mean, minimum and maximum irradiance values for each wavelength, as well as the standard deviation, coefficient of variation (CV) and amount of time that the irradiance was above various intensity thresholds. During these sampling events, an underwater video camera, recording at 15 frames s^{-1} was mounted on a frame with two fixed rulers held in front of the frame in the *x* and *y* planes of view of the camera. This frame was positioned on the seawater surface interface adjacent to the radiometer (but not interfering with the field of view). The frame-by-frame extracted digital video allowed the measurement of seawater interface wave amplitude and wavelength characteristics, as well as the determination of horizontal wave velocity to provide reference data for computational wave modelling validation.

Computational wave-lensing modelling, as described in Deckert and Michael (Deckert and Michael, 2006), was required to validate field measurements and assess the ability of the radiometer to measure wave-lensed pulses. The model was run at four different wavelengths (320, 490, 555 and 670 nm) for Morel Case I waters (representative of the Gulf of Eilat during the experiment) using model inputs of: zenith angle (6.8 deg), wavelength (1.2 m), amplitude (0.2 m), modelled photons (1×10^7), chlorophyll content (0.01 mg m^{-3}) and wavelength-specific absorption, scattering and surface albedo functions as fully documented previously (Deckert and Michael, 2006). Two-dimensional plots of wave-lensed irradiance were generated for photons incident at three angles to the wave crest (90 deg, crest; 45 deg, intermediate; 0 deg, crest parallel) binning at 1 cm^2 pixels.

Measurements of wave-lensing frequency on coral colonies (*N*=80) from a range of depths (1–10 m) in the Gulf of Eilat were made using aquatic video surveys acquired on a Canon Powershot 630 (Ohta-ku, Tokyo, Japan) at 15 frames s^{-1}. A 0.5×0.5 m quadrant was placed over a coral colony by a SCUBA diver, and the number of wave-lensed pulses incident on the coral was assessed over a recording period of 10 s. Information on the depth of each coral surveyed was collected from a dive computer, with the filming taking place at 45 deg to the vertical, to ensure that the diver's exhaust gas did not modify the surface wave and light field. Each video was decomposed into 15 individual frames per second, and the individual pulses were counted by a single operator.

In situ sprinkler irradiance measurements

Measurements of the effectiveness of sprinkler irrigation systems to remove wave lensing was tested using the PRR800 in the shallow waters adjacent to the IUI. A 2×2 m square frame, constructed of

25 mm black piping, was fitted with four spring-loaded 360 deg irrigation sprinklers (Hunter, San Marcos, CA, USA), which were suspended on the surface by four inner tubes of black tyres. Seawater was supplied to the sprinkler system using the IUI seawater pumps used for maintaining flowing seawater for the aquariums through two 25 mm supply hoses. The radiometer sensor was located 2 m below the surface in the centre of the sprinkler array. Alternating periods of sprinkler operation were then recorded by the PRR800 at a sample frequency of 15 Hz, close to solar noon on five separate days in July 2009. All the irradiance and wave-lensing measurements were collected when the wind speed was 2–3 m s^{-1}, with the subsequent wave surface conditions producing the most pronounced wave lensing (Dera and Stramski, 1986).

Sprinkler-tank experiments

Two coral species from the shallow waters of the Gulf of Eilat (<5 m) were used in this study: *Stylophora pistillata* (Esper 1797) and *Favites abdita* (Ellis and Solander 1786). Six colonies of *S. pistillata* were fragmented into 28 nubbins (each 8 cm long) and mounted on black plastic holders with a non-toxic glue. Twenty eight individual colonies (each 10 cm in diameter) of *F. adbita* were collected from the same sample location that were flat and with non-tissue-covered bases. Corals were transplanted to plastic stands in a running seawater tank (volume 400 l) and covered with shade cloth to enable recovery for 4 days at 275 μm quanta m^{-2} s^{-1} midday irradiance. Shade cloth was modified every 4 days to adapt the corals to higher light fields, with midday irradiance intensities of 575, 780, 1000, 1225 and 1500 μm quanta m^{-2} s^{-1}, respectively. Corals were then held a further 7 days without shade cloth at 2000 μmol quanta m^{-2} s^{-1} before being transplanted into treatment tanks.

The experimental design comprised 12 Perspex aquaria (volume 10 l) with running seawater and an air bubbler, nestled inside a larger coral table with running seawater at ambient temperature (Fig. 1A). The air bubbler created bubbles sufficiently large that small waves (amplitude ~1 cm) propagated across the tank to the exit drainage port on the far side of the tank (Fig. 1B). These waves were sufficient to create wave lensing in all tanks, with a frequency of ~300 lensed flashes per minute and a maximum pulse intensity of 5700 μmol quanta m^{-2} s^{-1}. Each tank had two *S. pistillata* nubbins and two *F. abdita* colonies resting on small plastic frames to allow water flow above and below the corals. The top surface of the coral was 8 cm below the surface for the *S. pistillata* nubbins and 11 cm below the surface for the *F. abdita* colonies. Four treatments were randomly distributed between the tanks, with three tanks per treatment. These treatments were: control (C), sprinkler (S), heated control (HC) and heated sprinkler (HS). The sprinkler treatments each had a small black 360 deg garden sprinkler mounted above the tank on a thin black wire, which produced 98% sprinkler coverage on each tank (Fig. 1B). Heated tanks comprised a small 100 W heater per tank, with supplemental heating coming from two sumps (capacity 230 l) that were heated with an 1800 W heater to the desired temperature. Seawater at ambient temperature would flow inside 20 m of tubing inside the heated tubs (Fig. 1A). The thin plastic piping facilitated adequate heat exchange with the surrounding warm water before being pumped through the sprinkler head or seawater pipe into each tank. Each heated treatment was warmed at 1°C per day for 4 days until the heated treatment reached 31°C and was maintained at 4°C above the control temperature for the 10 day experimental period. Temperature data from each treatment were logged every minute using PT100 platinum thermocouples logging to a four-channel PT-104 converter (Pico Technology Limited, St Neots, Cambridgeshire, UK), accurate to three decimal places from newly calibrated sensors. This information was relayed to a logging laptop for real-time display. Additional temperature measurements were also made with 12 Hobo 64 kb Temp/Light pendants (Onset Computer Cooperation, Pocasset, MA, USA), with one sensor per tank. All Hobo loggers were placed 10 cm below the surface waters in the tank to measure the light field to which the top surface of the corals would be exposed. In order to assess the photosynthetic apparatus of the coral symbiont, quantum yield measurements (F_v/F_m pre-dawn and $\Delta F/F_m'$ during midday) were made twice a day using a diving PAM (Heinz Walz GmbH, Effeltrich, Germany) with a new fibre-optic sensor. A spacer was fitted so that the fibre was positioned 5 mm from the highest apical surface of each coral nubbin before dawn and at solar noon. The same point on every coral was measured each day, allowing the most sun-exposed surface yields to be tracked throughout time. During the solar noon measurements, particular care was made not to shade the coral from ambient lighting conditions.

After the last diving PAM measurements were conducted at solar noon on day 10, the coral fragments were removed from the treatment tanks and dark acclimated for 30 min before coral photo-

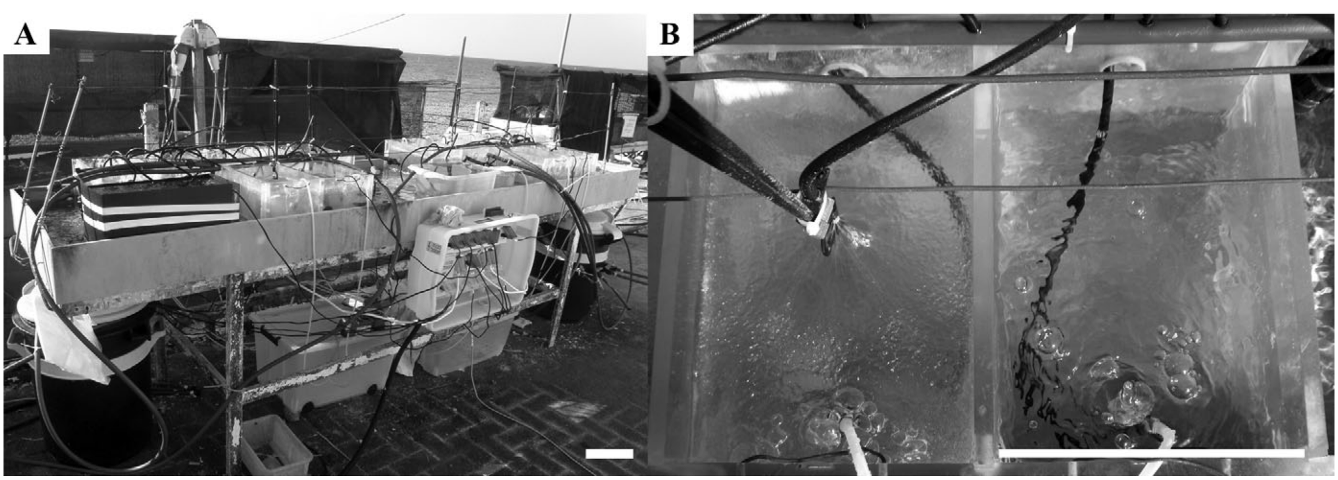

Fig. 1. (A) Photograph of the tank-based wave-lensing experiment with 12 tanks randomly distributed around the coral table. Air bubbles were supplied from air pumps, and heated water was pumped through heating bins (left and right of image) *via* black tubing to tanks and sprinkler heads. (B) Close-up of the sprinkler and control conditions with visible wave lensing. Scale bars: 10 cm.

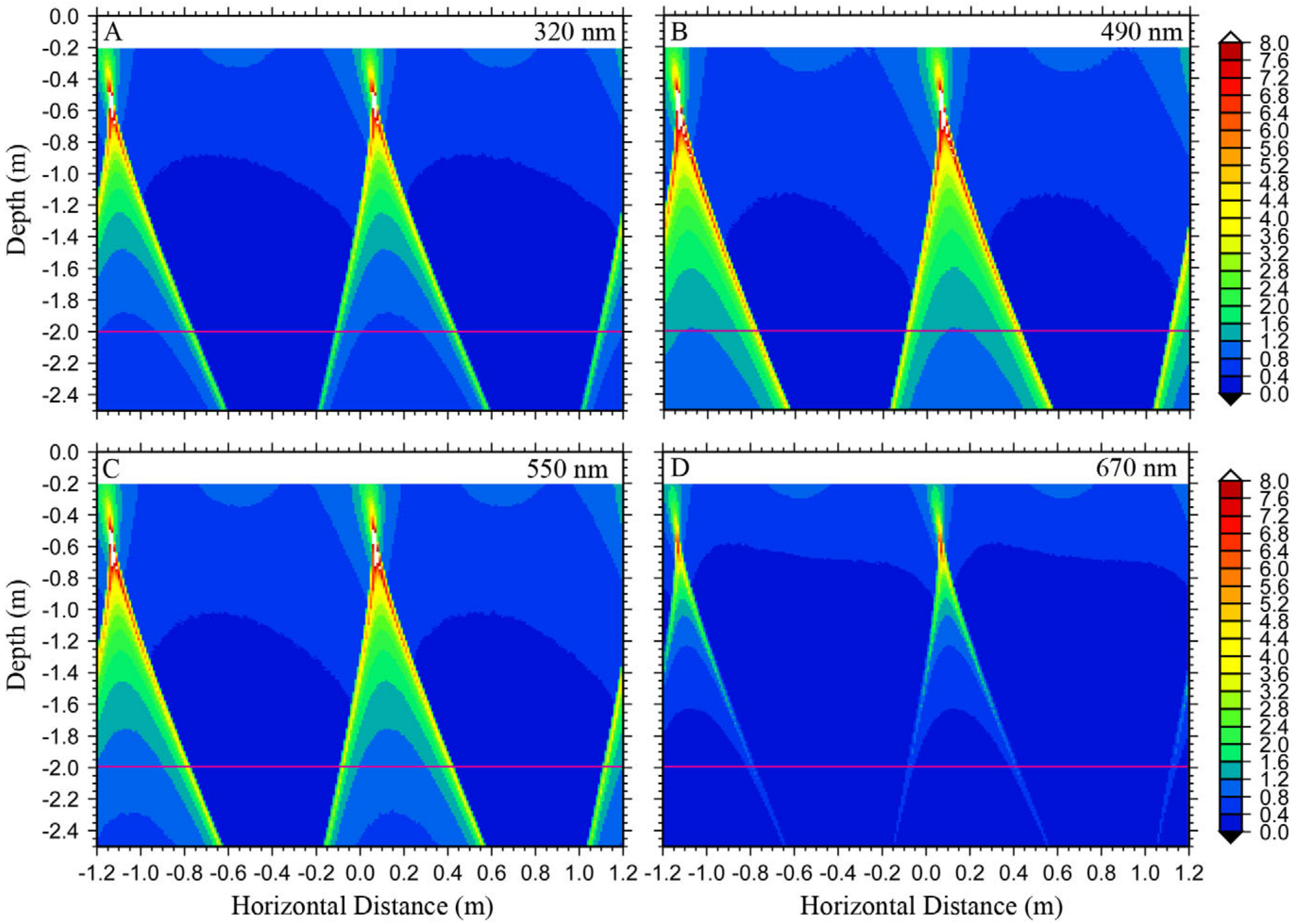

Fig. 2. Two-dimensional modelled wave-lensing environment for the field wave-lensing conditions for Eilat at four different wavelengths, with photons incident from vertically above the wave crest at: (A) 320 nm, (B) 490 nm, (C) 550 nm and (D) 670 nm. The colour bar indicates the modelled irradiance levels above surface irradiance intensities. The red line indicates the depth of the PRR800 to provide reference to actual measured irradiance values.

physiology was acquired using an imaging PAM (Heinz Walz GmbH, Effeltrich, Germany). Measurements of absorption, maximal quantum yield (F_v/F_m) and electron-transport rates (ETRs) (gained from rapid light curves) were performed on all corals from the same measured point on the coral outlined in the diving PAM measurements. Destructive coral physiology measurements were made only on the *S. pistillata* fragments as permits could not be obtained for destructive sampling of the *F. abdita* coral. Coral nubbins were airbrushed using filtered (0.45 μm) seawater, and the chlorophyll *a* (chl *a*) was extracted using methods outlined previously by Winters and colleagues (Winters et al., 2009). Total and host protein were determined using a Bradford Protein Analysis kit (Bio-Rad Laboratories, Hercules, CA, USA) following Bradford (Bradford, 1976). The surface area of each coral skeleton was determined using the single wax-dipping methodology outlined by Veal and colleagues (Veal et al., 2010).

Oxygen evolution

The net oxygen production and consumption rates were measured using a real-time membrane-inlet mass spectrometer (MIMS QMS 200 Pfeiffer vacuum, Asslar, Germany) attached to a small (3.3 ml), custom-made climate-controlled chamber containing a small specimen of the target organism. Measurements of the concentrations of the target elements ($^{16}O_2$ and $^{18}O_2$) and two reference elements (^{14}N and ^{40}Ar) were recorded at 1 Hz. Photosynthesis was calculated based on the measured evolution of $^{16}O_2$ in the chamber water, whereas respiration was calculated based on the measured decline in $^{18}O_2$ after a spike of this element was added to the water (amounting to ~1% of the total dissolved oxygen). All the measurements were replicated with 10 specimens of *S. pistillata* under flow conditions, both in the dark and under conditions of static and flashing light. Flow was generated in the chamber using a small stirrer. The temperature of the seawater in the chamber was maintained at 25°C using a water jacket connected to a temperature-controlled water bath. A 150 W cold light source (Schott KL 1500, Mainz, Germany) was used for illumination, in conjunction with the PT100 actinic light source of the Dual PAM (Heinz Walz), and a 5 W mains-powered variable-intensity LED power source provided flashing illumination at 2400 μmol quanta $m^{-2} s^{-1}$ at 3.3 flashes per second. The average illumination under both flashing and constant illumination was the same, measured as 1630 μmol quanta $m^{-2} s^{-1}$, with the 4π irradiance sensor of the Dual PAM inside the chamber filled with seawater. Coral fragments were frozen in liquid nitrogen after testing. Frozen samples were then airbrushed 1 day later, as outlined previously, to determine the concentration of protein and chl *a*.

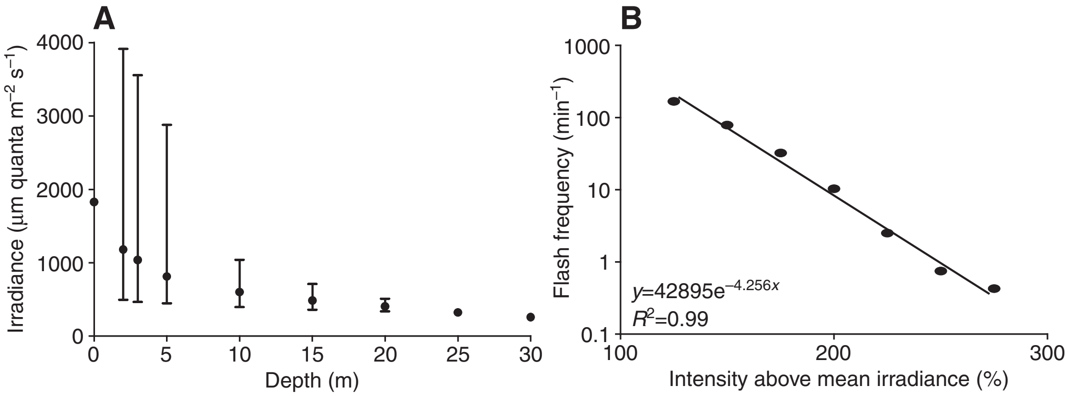

Fig. 3. (A) Mean, minimum and maximum irradiance recorded at depths between 2 and 30 m from the waters adjacent to the coral reef slope in the Gulf of Eilat under conditions of light wind (3.7 m s^{-1}). (B) Irradiance intensity above the mean level at depth, expressed on a log scale, versus flash frequency received per minute, recorded from a depth of 1.5 m under conditions of light wind (2 m s^{-1}) in the shallow waters of the Gulf of Eilat.

Statistical analysis

Statistical analysis was performed with XLStat (Addinsoft SARL, Paris, France). Linear and exponential regressions were fitted when statistically significant. ANOVA was performed to determine the effect of the treatments, with a *post hoc* Tukey's test used to determine statistically significant groups within the ANOVA.

RESULTS

Wave-lensing model and instrument suitability

Wave-lensing model results from the Deckert and Michael model (Deckert and Michael, 2006) revealed that, under average wave conditions occurring in Eilat, the peak wave-lensing focal point was ~0.5 m below the surface of the water (Fig. 2). The field radiometer measurement started at a depth of 2 m, indicated by the purple line in Fig. 2. At any instant in time, a wave-lensed pulse of irradiance (>250% surface irradiance intensity) would be 3.4 cm wide in cross-section on the top of the 2π collector of the PRR 800 radiometer (which has a diameter in cross-section of 1.21 cm). With a wave velocity of 0.6 m s^{-1}, it would take 57 ms for the pulse to transit the collector, which is less time than the 50 ms integration time of the radiometer. These modelled results would indicate that the PRR 800 radiometer would be able to measure wave-lensed pulses accurately up to 5525 μmol quanta m^{-2} s^{-1}, which is 2.5 times the average midday surface irradiance values for summer in Eilat.

Field measurements

During the study period, the average temperature of the seawater was 26.9±0.3°C, and the site received an average midday irradiance of 2211±49.4 μmol quanta m^{-2} s^{-1}. Between the sunlight hours of 06:00 to 18:00 h for the three months of the study, wave-lensing conditions (defined by wind speeds of 2–7 m s^{-1}) were present for 55.6% of the time. Attenuation profiling conducted in the coastal waters adjacent to the coral reef revealed a very low $K_{d(PAR)}$ of 0.055, in line with reports of high water clarity in the Gulf of Eilat, even in shallow near-shore waters. Measurements of the wave-lensing variability around solar noon on 6 July 2009 during ideal wave-lensing conditions with light winds (3.9 ms^{-1}) (Fig. 3A) indicated that there was still 10% variability in the mean downwelling PAR irradiance at a depth of 30 m. In shallow waters, maximum irradiance levels at a depth of 5 m can exceed the surface intensity, and measurements at 2 m reveal maximum irradiance values in excess of 3900 μmol quanta m^{-2} s^{-1}, twice the surface irradiance levels and nearly three times the mean irradiance at that depth. Timed measurements of wave lensing collected at a depth of 2 m at solar noon on 27 July 2009 (Fig. 3B) revealed that the ratio of flash frequency to flash intensity per minute is exponential, with an average of 100 flashes above 150% mean irradiance and less than one flash every minute above 250% mean irradiance, with an intensity in excess of 3950 μmol quanta m^{-2} s^{-1}. Measurements of visually observed light caustics interacting with living corals, collected from varying depths, are displayed in Fig. 4, depicting a significant linear trend towards an increasing number of pulses with depth due to a greater amount of caustic intersection and blurring caused by optical scattering. Deeper than 7 m, it was not possible to detect individual caustics owing to poor substrate contrast making visual identification ineffective.

When the sprinkler frame was moved over the top of the sensor and activated, there was a 5.0% reduction in downwelling visible irradiance (Fig. 5A), with slightly greater reductions of 7.5% in the ultraviolet part of the spectrum, although the spectral differences were not statistically different. The sprinklers also significantly decreased the CV (ANOVA, $F_{1,23950}$=33.519, P<0.0001), which is an expression of the variance in the irradiance data, by 460% in the ultraviolet and nearly 500% in the visible range of the spectrum. If this information is then expressed as the period of time each minute the downwelling irradiance was

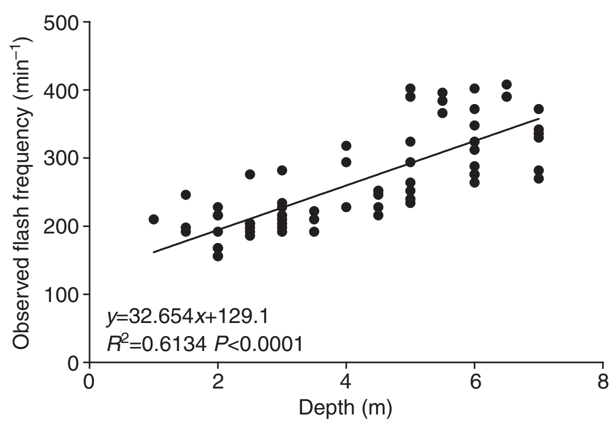

Fig. 4. Visually observed wave-lensing flashes per minute measured from the surface of a range of common morphologically diverse corals found in water of depths of 1–7 m in the Gulf of Eilat.

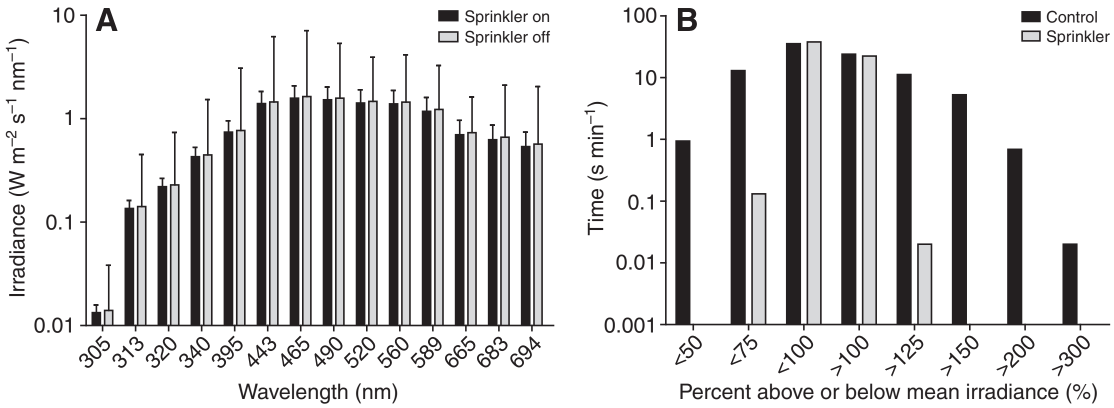

Fig. 5. (A) Multispectral irradiance levels from 305 to 694 nm recorded with the PRR800 situated at a depth of 1.5 m while the sprinklers where turned on (black) and off (grey) under conditions of light wind (2 m s^{-1}). This is plotted against the mean ± s.d. irradiance intensity (W m^{-2} s^{-1} nm^{-1}) expressed on a log scale. (B) Time spent above or below the mean irradiance measured at solar noon in 1.5 m of water under conditions of light wind (2 m s^{-1}) under both control (black) and sprinkler (grey) conditions, expressed as seconds per minute at each level on a log scale.

above or below the mean irradiance at depth (Fig. 5B), the results reveal that, for control conditions (with no sprinkler), the irradiance would exceed 125% for 11.2 s every minute, with less than 1 s every minute above 200%. Interestingly, during that same minute, the light-field also spent nearly 13 s below 75% mean irradiance, in comparison with when the sprinkler was operated, when only 130 ms per minute were below 75% and 16 ms above 125% mean irradiance.

Tank experiments

Irradiance measurements in the visible spectrum collected from the light and temperature loggers revealed that the sprinklers reduced the downwelling photosynthetically active irradiance received by the corals by 4%, similar to the field results, with a 250% reduction in the coefficient of variance. Temperature data collected from each treatment, when compared with those from the platinum thermocouples, revealed that the Hobo light and temperature loggers were being excessively heated above the ambient water temperatures by absorption of incident radiation. The heating anomaly tracks the irradiance profile, as displayed in Fig. 6, with positive temperature biases in excess of 3°C occurring around solar noon. The abrupt drop in the temperate anomaly at 16:30 h was due to the treatment tanks becoming shaded by adjacent buildings and the terrain, thereby cooling to correct ambient water temperatures. Thermal shielding of the sensors was not possible as it would have also obscured the irradiance detector.

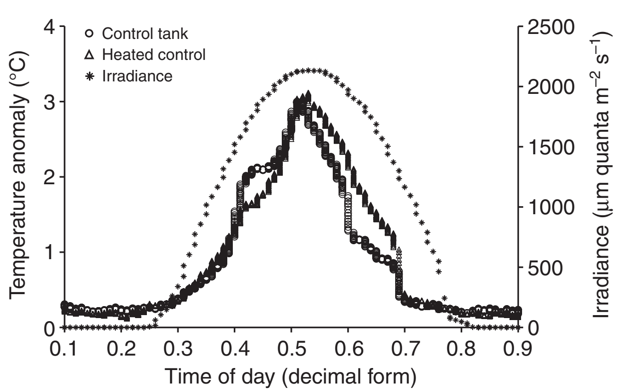

Fig. 6. Daily temperature anomalies above ambient water temperature recorded by the Hobo temperature loggers for both the control (circle) and heated control (triangle) treatments due to solar warming, with solar irradiance (star) plotted on the second *y*-axis expressed in units of μmol quanta m^{-2} s^{-1}.

Predawn assessment of photosystem II activity, used as an indicator of chronic photoinhibition, revealed gradual reductions over time under most treatments for both species; however, none was statistically significant. Both the control and heated *S. pistillata* sprinkler treatments consistently produced a higher yield than that of the control groups. A similar trend was detected for *F. adbita*. The HS treatment constantly scored higher yields, yet the S and C treatments performed the same. The imaging PAM results did not reveal any statistically significant groups within the four treatment groups, similar to the diving PAM results. The rapid light curves information from the noon-sampled *S. pistillata* revealed that the photosystem was saturated above 500 μmol quanta m^{-2} s^{-1}, possibly explaining the lack of statistical difference, and both wave-lensed and sprinkler treatments were operating at light intensities above saturating irradiance levels.

Physiology

There was no significant difference in the concentration of chl *a* per zooxanthella cell among the treatments (ANOVA, $F_{3,16}$=1.487, P=0.256); however, both the S and HS treatments were slightly elevated compared with their relative controls (S and C) (Fig. 7A). The analysis of total protein per surface area (Fig. 7B) revealed a significant effect of treatment (ANOVA, $F_{3,16}$=6.725, P=0.004), with the *post hoc* Tukey's test revealing that the sprinkler treatment had significantly less protein than all other treatments (P<0.05). In both the zooxanthellae cells to host protein (ANOVA, $F_{3,16}$=13.082, P<0.0001; Fig. 7C) and to surface area comparisons (ANOVA, $F_{3,16}$=10.121, P=0.0001; Fig. 7D), the heated control had significantly more zooxanthellae than the other treatments, with decreases in both S and HS treatments compared with the respective controls.

Gross oxygen evolution

Gross oxygen evolution under both flashing and constant illumination with the same total photon flux revealed no statistically significant difference between treatments, when normalised to the amount of chl *a* and chl c_2 per cm^2. All the nubbins used in the experiment were of a similar size and, despite being collected from the same depth and same time of year (within 1 day of each other),

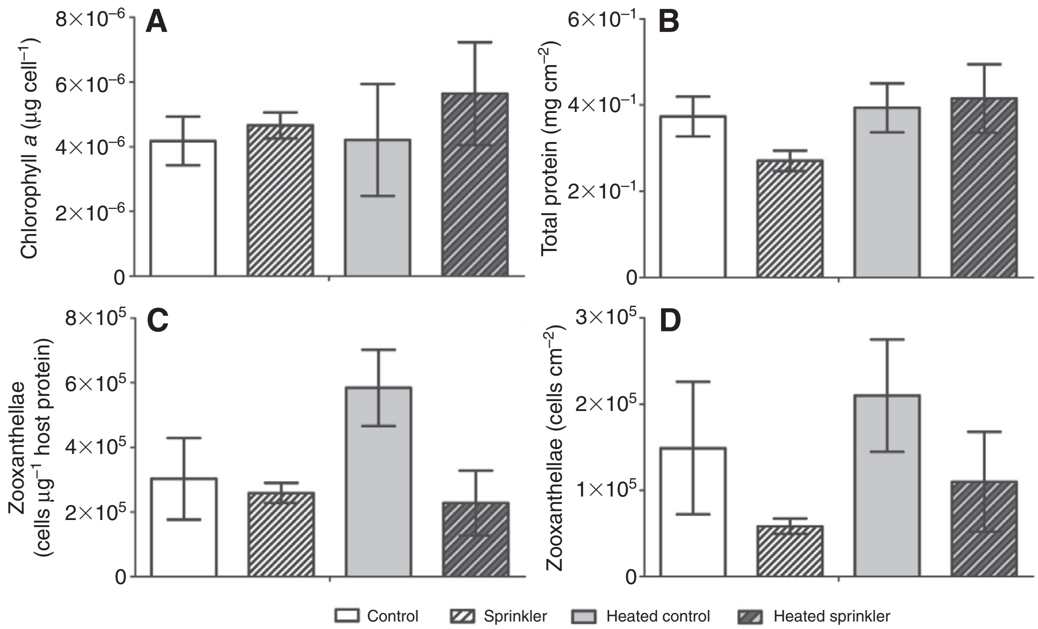

Fig. 7. Physiological parameters of *Stylophora pistillata* for each treatment: control (white), sprinkler (white with lines), heated control (grey) and heated sprinkler (grey with lines) for (A) chlorophyll *a* (µg) per zooxanthellae cell, (B) total protein (mg) per surface area (cm^2), (C) zooxanthellae cells per host protein (mg) and (D) zooxanthellae cells per surface area (cm^2).

there was a significantly variable chlorophyll content. These findings support the other results presented in this research from both the PAM and coral physiology data.

DISCUSSION

The northern section of the Red Sea features the highest-latitude coral reefs in the world. Despite the fact that the area is a long way from the Equator, the corals in the Gulf of Eilat (Aqaba) receive, on average, 40% higher irradiance than lower-latitude tropical reefs elsewhere in the world (Winters et al., 2009). These high irradiances are a result of the unique environment of the northern Red Sea, where desert (with associated cloudless skies) surrounds a deep semi-enclosed gulf, with low nutrient input creating meso-oligotrophic water conditions similar to that of oceanic waters (Stambler, 2006). The Gulf of Eilat has strong summer thermal stratification and nutrient depletion of the upper 60–80 m of water, resulting in very low attenuation coefficients [$K_{d(PAR)}$=0.04] with a euphotic zone reaching from 80 to 115 m, producing one of the clearest coastal water bodies in the world (Stambler, 2006). Wave lensing of surface irradiance was detected during this study to a depth of 30 m, with over 10% variability in the mean irradiance at this depth during solar noon. Previous studies have reported similar variability from 30 to 40 m (Stramska and Dickey, 1998; Morel et al., 2007); however, in both cases, the intensity of the flashes was less than 150% mean irradiance. During this study, wave lensing above 150% mean irradiance was recorded down to a depth of 20 m, which is the deepest currently reported in the literature. The conditions during which measurements were conducted were ideal, with the maximum number and intensity of light flashes taking place with winds between 2–5 m s^{-1} (Dera and Stramski, 1986). Under these field conditions, corals at a depth of 2 m of water were experiencing 80 pulses per minute above 2350 µmol quanta $m^{-2} s^{-1}$, 15% higher than surface irradiance values. The log-normal distribution of irradiance intensity with frequency present in this study has also been found in other experiments (Dera and Stramski, 1986), caused by the loss of beam collimation owing to the scattering of light along a longer path in the water. Despite this, with depth, there is a greater intersection of light caustics from other waves (Zaneveld et al., 2001), resulting in higher numbers of observed caustics moving across a coral. Deeper than 7 m, this pattern will break down as there will be excessive blurring to the point of indistinction by the human eye; however, as indicated previously, this variability extends to depths deeper than 40 m, which represents the depth range of the majority of coral species found in the Gulf of Eilat.

Stylophora pistillata is one of the most dominant corals in the Red Sea, occupying a large depth range from 1 to 65 m (Loya, 1972; Loya, 1976). The adaptation of *S. pistillata* to these high-light environments has been demonstrated previously, with their zooxanthellae being smaller in diameter and located deeper inside the host tissue when compared with zooxanthellae from low-light corals (Winters et al., 2009). The shallow *S. pistillata* has also been shown to host predominately clade a zooxanthellae, which has been suggested to be more thermally tolerant than other clades commonly found inside corals (Winters et al., 2009). Previous work by Winters and colleagues has revealed that (mean) irradiance is the main driving force for physiological change in *S. pistillata* in the Gulf of Eilat (Winters et al., 2003). As the use of sprinklers did not create a large reduction in irradiance, the absence of a measured change in the photophysiology of the corals was therefore not unexpected. The higher F_v/F_m yields for the heated treatments compared with the ambient were also noted by Winters and colleagues (Winters et al., 2009), with similar observed pre-dawn F_v/F_m and afternoon photoinhibition hysteresis (Winters et al., 2003).

The response of shallow-water corals to dynamic irradiance intensities is very poorly understood, with most research being conducted in laboratory conditions (Shubert et al., 2001). Fietz and Nichlisch proposed that acclimation of a photosystem to fluctuating light is a response type outside the known schemes of high- and low-light adaptation (Fietz and Nichlisch, 2002). Unlike sunflecks in traditional terrestrial and marine canopy environments (Logan et al., 1997), where a significant amount of daily irradiance resources comes in brief periods of high exposure to light (Adams et al., 1999), wave lensing is at the other end of the scale, characterised by very high-intensity pulses occurring very rapidly with supersaturating intensities. Marine macroalgae in the wave-swept zone display this pattern of light-utilisation curves, suggesting an adapted photosystem matching the frequency of wave-induced light flashes, although little can be inferred about the mechanism (Wing and Patterson, 1993). The body of literature from the phytoplankton community is mixed in terms of the response of phototrophs to wave lensing, with the general trend reporting an increase in photosynthetic efficiency, when the pulses occur between limiting and saturating intensities, with negative trends above saturating intensities (Walsh and Legendre, 1982; Dromgoole, 1988; Litchmann, 2000). As the sprinkler droplets did not cause a marked reduction in downwelling irradiance, as roughened water surfaces do not increase in reflectivity at moderate-to-high solar elevations (Kirk, 1994), and the wave-lensing variability was above the saturating intensity of *S. pistillata*, the indistinguishable response of the coral between sprinkler and control treatments was expected.

The presence of apparently healthy corals in the shallow-water regions of the world's coral reefs clearly demonstrates their ability to adapt to the dominant frequencies of their environment (Legendre et al., 1986). The responses of phototrophs to fluctuating light are observed from the level of chloroplasts, up to organs, and to the entire plant (Nedbal et al., 2007). Shallow corals are known to have a variety of mechanisms to deal with excess light energy (Gorbunov et al., 2000). The main mechanism reported that can consist of up to 80% of the total energy dissipation is through non-photochemical quenching (NPQ) on all its components. It is interesting to point out that these processes are characteristically measured on a time-scale of minutes, whereas the high-light frequency is perhaps two- to threefold faster (Fig. 4). This might lead to the assumption that the key process in photoprotection of shallow-water corals is not NPQ; instead, it is a massive reduction–relaxation of the plastoquinone pool on the order of milliseconds. We did not note any significant difference in gross photosynthesis between the sprinkler treatment and the control samples; however, we postulate that this was possibly due to the special ability of corals to mitigate instantaneous extremely high irradiance fluxes by rapid photochemical quenching redox cycling. This question requires further experimentation and analysis in the future.

The mechanism for photosynthesis and protection from harmful light stress under these incredible conditions is yet to be fully understood and requires further investigation. These systems of corals to mitigate high light stress would appear to be unique to the marine phototrophic world as irradiance levels in excess of 2500 μmol quanta m^{-2} s^{-1} and variability of over 300 pulses per minute are not possible in terrestrial environments, yet are regularly received by shallow-water corals. The corals in this study appeared to be photophysiologically unaffected by the wave-lensing conditions and suitably equipped photosynthetically to handle the dominant light frequency and intensity of their surrounding environment.

LIST OF SYMBOLS AND ABBREVIATIONS

C	control
chl *a*	chlorophyll *a*
chl c_2	chlorophyll c_2
CV	coefficient of variance
F_v/F_m	maximum quantum yield of photosystem II
HC	heated control
HS	heated sprinklers
NPQ	non-photochemical quenching
PAM	pulse-amplitude-modulated
PQ	photochemical quenching
S	sprinkler

ACKNOWLEDGEMENTS

We acknowledge the assistance from the Interuniversity Institute for Marine Science technical Staff for plumbing and electrical support. We also thank Oded Ben-Shaprut and Genadi Zalzman for marine support and David Iluz for allowing us to borrow his PRR800 for our research. Modelling used in this manuscript was kindly provided by Rudolf Deckert. This manuscript has benefited significantly from the anonymous feedback of three reviewers. This research was part-funded through an Australian Research Council industry linkage with the US National Oceanic and Atmospheric Administration (to O.H.-G.) as well as the 2009 Australian Israeli Scientific Exchange Foundation (AISEF) (to C.J.V.).

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