RESEARCH ARTICLE

Light from down under

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SUMMARY

Coral–algae symbiosis is a key feature of tropical corals and is highly dependent on the efficiency with which solar energy is attenuated by the coral. Scleractinian corals are among the most efficient light collectors in nature because of the modulation of the internal light field in the coral skeleton. Interestingly, coral skeleton particles composing the sandy bottoms in reef margins sustain these optical characteristics. In the present study, we examined two free-living coral species – *Heterocyathus aequicostatus* (Caryophyllidae) and *Heteropsammia cochlea* (Dendrophylliidae) – common on biogenic coarse carbonate sand of the Great Barrier Reef but absent from fine sand at the same depth. In coarse carbonate sand, light penetrates a few millimeters below the surface and propagates along horizontal distances of a few centimeters. In fine sand, almost all of the light is reflected back to the water column. For photosynthetic sand-dwelling organisms such as the studied species, with over one-third of their surface area facing the substrate, light flux to their underside may be beneficial. A correlation was found between the diameter of these corals and the distance that light may travel in the sand under the coral. Laboratory and field measurements show that the symbiotic algae on the underside of the corallites are photosynthetically active even when the coral is partially buried, implying sufficient light penetration. Other organisms in the study site, such as fungid corals and foraminiferans, with different morphologies, have different light-trapping strategies but are also photosynthesizing on their underside. The importance of the substrate type to the performance of the three main partners of the symbiosis (coral, endosymbiotic algae and a sipunculan worm) is highlighted, and is a striking example of co-evolution.

Key words: coral, light, Great Barrier Reef, *Heterocyathus*, *Heteropsammia*, *Aspidosyphon*.

INTRODUCTION

The distribution of reef-building (hermatypic) corals is limited primarily by the availability of photosynthetic active radiation (PAR) (Gattuso et al., 2006) because of the requirement for minimum light levels by zooxanthellate corals. Hence corals are dependent on the efficiency with which they collect solar energy (Enríquez et al., 2005). Indeed, symbiotic scleractinians are among the most efficient solar energy collectors in nature. Enríquez et al. (Enríquez et al., 2005) suggested that modulation of the internal light field by the coral skeleton may be an important driving force in the evolution of scleractinians. Coral skeletons are efficient bulk scatterers (Stambler and Dubinsky, 2005), scattering in all directions (Smith, 1966), allowing propagation of light over relatively long distances.

In shallow water, where the depth is much less than the potential for light to penetrate, a large fraction of the subsurface light reaches the ocean floor, where portions of the light energy are absorbed or reflected back into the overlying water column (McFarland and Munz, 1975). Many shallow bottoms are nearly-Lambertian surfaces (diffusive surfaces that have constant brightness regardless of the angle viewed) where the detected radiance is independent of the viewing angle. This is even more pronounced in reef margins, where the seafloor consists of coral fragments and carbonate sand. Where benthic communities add structural complexity, pigmentation and heterogeneity, the seafloor reflectance, measured on scales of

centimeters, is different from a Lambertian surface (Mobley and Sundman, 2003), hence growth of macroalgae, turf algae or microbial mats might change the reflectance of soft bottom.

Sandy-bottom areas adjacent to coral reefs of the Great Barrier Reef (GBR) cover a vast area but they receive little attention in the literature compared with coral reef hard substrate. Soft-bottom areas are often considered a marine desert because of their relative instability and low structural complexity. However, these habitats offer space and resources for various organisms. Light availability and bottom stability may determine the nature of the community and richness of scleractinian coral species in sandy areas.

In the present study, we examined two free-living coral species, *Heterocyathus aequicostatus* Milne Edwards and Haime 1848 (Caryophyllidae) and *Heteropsammia cochlea* (Spengler 1781) (Dendrophylliidae), inhabiting carbonate sand habitats of the GBR. Depending on the physical forces in their habitat, these species are found partially buried (5–10 mm in the sand). We examined the special symbiosis of these corals with one species of sipunculid – *Aspidosiphon jukesii* Baird 1873 – and their mutual strategy to occupy these sandy, relatively unstable areas.

This fascinating symbiosis (Pichon, 1974) initiates when a coral planula larva settles on a micro-gastropod shell already inhabited by a sipunculan worm. As the sipunculan grows and the shell becomes too small to shelter it, the coral provides the necessary

protection by growing around the protruding worm to form a sclerenchyme extension in continuation of the shell.

Heterocyathus aequicostatus and *Heteropsammia cochlea* are exclusively known from the Indo-Pacific. While these corals have received wide attention (for a review, see Stolarski et al., 2001), their light-trapping abilities have not been studied. We therefore designed the present study to determine how these corals survive and their zooxanthellae photosynthesize while in relatively deep environments and often partially buried in the sand.

MATERIALS AND METHODS
Study location

The area selected for this study is located to the north of Wistari Reef near Heron Island (Capricorn Bunker group of islands, southern GBR, 23°27′S, 151°54′E). This site was selected following an earlier record (Fisk, 1981; Fisk, 1983) of high abundance of the studied species. Because of the presence of Wistari Reef and the channel that is created between Heron Island and Wistari Reef, strong tidal currents flow in an east (ebb tides) to west (flood tide) direction. The channel experiences the strongest tidal currents in the Capricorn Bunker group of islands, with spring tide currents exceeding $1.5\,\mathrm{m\,s^{-1}}$ close to the reef (Maiklem, 1968; Pickard et al., 1977).

Survey

A survey of *H. aequicostatus* and *H. cochlea* at Wistari Reef was performed at a depth range of 15–30 m. Four transects were set perpendicular to the reef flat of Wistari Reef to determine the distribution of the study corals at the study site and their habitat preferences. Each transect comprised four diving sites, one each at depths of 15, 20, 25 and 30 m. At each dive site, an area of ~50 m radius around the anchor was surveyed. The density and size of *H. aequicostatus* and *H. cochlea* as well as other coral species were recorded and a sample of sand (three tubes of 50 ml) was taken for granulometric assessment. The pre-dried sediment was passed through a series of sieves and each fraction of the sample between successive sieve sizes was determined by weighing.

Light measurement

In situ light measurements were performed using a Li-Cor light meter (LI-189, Li-Cor, Lincoln, NE, USA) equipped with a cosine-corrected underwater quantum sensor (LI-192, Li-Cor), collecting light from a whole hemisphere. Downwelling and upwelling light measurements were preformed at mid-day during calm seas by a SCUBA diver with the light meter pointing up (downwelling light) or down (upwelling light). The sensor was aligned against a vertical line hanging from a buoy (attached downwind of the boat) and attached to a heavy floating weight (not reaching the sea floor, to prevent suspension). At the sea floor (25–28 m deep), back-scattered light measurements were also performed with the light sensor facing the sand, touching it and also buried horizontally, under approximately 1 cm of sand. This was performed first on a coarse coral carbonate sand, and then, on the same day (1 h later) and under similar light conditions, at a second site with similar depth (25–27 m), this time on 'regular' fine sand substrate. Because we were mostly interested in the responses of symbiotic dinoflagellates to light, we integrated the light intensity over PAR in the range of 400–700 nm. For light measurements in the laboratory, we used a spectrometer (S2000, Ocean Optics, Dunedin, FL, USA) equipped with a 600 μm UV-Vis optical fiber, providing an operational spectral range of 300–850 nm. The sensor's light integration durations were set to make maximal use of the dynamic range of

the sensor during each measurement session. Responses at different integration times were pre-calibrated. To correct for possible fluctuations, each measurement consisted of an average of several recordings with a total duration of no less than 1 s. All measurements were automatically corrected for electrical noise, and dark measurements, taken during each session and at each of the integration settings, were used to correct for other noise sources. All measurements were carried out underwater with the end of the fiber, as well as the specimen, submerged in seawater. For reflection measurements, a 15 deg acceptance angle restrictor was attached to the end of the fiber. Samples were placed 3 cm away from the end of the fiber, thus limiting the measurement area to $0.5\,\mathrm{cm^2}$. By pointing a thin-beam red-light laser pointer to the edges of the measured area and looking for the record of the red light on the spectrometer, we ensured proper positioning of the specimen in the measured area, prior to the actual measurements. In reflection measurements, a flat white Teflon standard was used as near 100% reflection. For measurements of light reaching the coral's interior, a 3 mm in diameter hole was drilled in the coral from its upper side, to which the end of the optical fiber was inserted. Black clay was used to prevent light leakage through the back of the fiber. Holes were drilled to measure the light reaching the central and sides of the bottom of the coral, and within the coral at its side (measuring scattering of light within the lower part of the skeleton). To examine the source of the light reaching the bottom or inner parts of a coral, measurements were repeated with different parts of the coral covered with black clay. Illumination was provided by a metal-halide lamp, which provides a broad-spectrum light including the short end wavelengths. Long wavelength enrichment was provided by a tungsten lamp.

To examine propagation of light underneath the coral, a physical linear model was created. The model consisted of a large reflecting (opaque) flat white or black plastic sheet (a rectangle covering over 100 mm in each direction of each measuring point, except for the illuminated edge) with six 3 mm diameter holes drilled at increasing distances from its edge (at 5 mm increments until 30 mm). Light was measured with the sensor positioned in the holes (as measured under the coral) as well as outside the model with the sensor placed ~1 mm above the substrate (measuring reflected light with the proper setting of the sensor). Holes not used during measurements were blocked to prevent light penetration through them. The entire experimental area had semi-uniform illumination (several light sources evenly spaced throughout the tank), though the settings ensured that light to the measurement points arrived only from the edge of the plastic sheet.

Substrate preference

To examine the preference for coarse or fine sand by the symbiotic sipunculid *A. jukesii*, we set up an aquarium (50×80 cm, 200 liters) with flow-through water and a 12 h:12 h light:dark regime (same light used for the light-scattering measurements). Half of the bottom of the aquarium was covered with freshly collected (but washed) substrate from Site 1 (coarse sand) and half with substrate collected at Site 2 (fine sand). We put five specimens of *H. aequicostatus* and five of *H. cochlea* on each of the substrates. The location of the specimens was monitored twice a day for 4 days. This was repeated three times, each with a different set of individuals (*N*=30 in total).

Phototaxis

To examine whether *H. aequicostatus*, *H. cochlea* and *A. jukesii* present phototaxis to maintain their position with respect to sufficient PAR, we set up an aquarium (50×80 cm, 200 liters) with flow-

through water and freshly collected (washed) substrate. A 12 h:12 h light:dark regime $(250\,\mu E\,m^{-2}\,s^{-1})$ was applied to half of the aquarium while the other half was constantly covered with black plastic such that almost no light penetrated. Five specimens of *H. aequicostatus* and five of *H. cochlea* were put in the center of the dark or light areas of the aquarium (five in each side) and followed for 3 days. Three times a day the location of the corals was scored. This 3-day procedure was repeated three times, each time with a different set of individuals.

PAM fluorometry

To study the photosynthetic capacity of symbiotic dinoflagellates in the examined species, dark-adapted maximal quantum yield (F_v/F_m) was measured using a pulse-amplitude modulated (PAM) fluorometer (Walz, Effeltrich, Germany) on the upper and bottom part of each individual ($N=10$) after a 30 min dark adaptation. In each measurement, the tip of the PAM main optical fiber was placed on the coral surface. We repeated this procedure on individuals that were reared for 2 months in aquaria with fine sand only and compared their photosynthetic performance with that of individuals kept on coarse sand. Aquaria were kept in a flow-through system under a light intensity of $50\,\mu E\,m^{-2}\,s^{-1}$. For comparison, we repeated the PAM measurements on other autotrophic organisms living in the same area: the fungid coral *Cycloseris cyclolites* and the foraminiferan *Marginopora* sp.

RESULTS
Survey

Density of *H. aequicostatus* and *H. cochlea* varied along a depth gradient, first appearing at 22 m at densities of 5 and 30 specimens m^{-2} for *H. aequicostatus* and *H. cochlea*, respectively, and peaked at 26 m (25 and 200 m^{-2} for *H. aequicostatus* and *H. cochlea*, respectively) but only on coarse carbonate sand. None were recorded on fine sand, regardless of depth. Mean grain size (Krumbein's phi scale) in the high-density area (coarse sand) was -0.92 ± 0.80; 52% was composed of granules, 35% of very coarse sand, 11.55% of coarse sand and 1.45% of medium sand (Fig. 1). The distribution of the two species along a depth gradient coincided with that reported by Fisk (Fisk, 1981), as did the ratio between densities of *H. aequicostatus* and *H. cochlea*, but total densities were lower than previously reported.

Light measurements

Downwelling diffuse attenuation coefficients in the open waters of the study site, north of Wistari Reef, reached 0.099 m^{-1} above the coarse sand sea floor and 0.12 m^{-1} above the fine sand sea floor, hence only 5–8% of the light available at the surface reached the sea floor at 25 m. Both coarse and fine sand reflect much of the downwelling light. This high reflection was measured both *in situ* (20 and 40% from coarse and fine sand, respectively) and in the laboratory ($27\pm3\%$ and $40\pm5\%$ from coarse and fine sand, respectively), adding to our confidence in the validity of the methods used. Light availability to the endosymbiotic zooxanthellae located on the underside of the corals, facing the sand, largely depends on two factors: (1) the type of sand (coarse or fine) and (2) the radial distance from the edge of the coral. On fine sand, virtually no light reached the bottom of the corals, ranging from 0.3–0.6% of the downwelling light at the very edge to 0.01–0.002% of the light at the center for *H. aequicostatus* and *H. cochlea* ($N=6$). On coarse sand, the availability of light at the bottom of the coral was much larger: 11–22% of the downwelling light at the edge of *H. aequicostatus* and *H. cochlea* ($N=6$). Even in the center of the
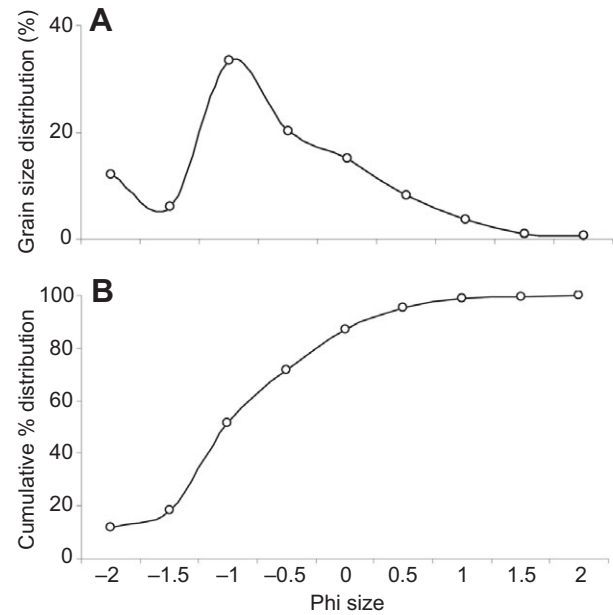

Fig. 1. Grain size distribution (A) and cumulative percent distribution (B) at the locations of peak *Heterocyathus aequicostatus*, *Heteropsammia cochlea* abundance at north Wistari Reef. Over 80% of the white carbonate grains at the site are larger than 1 mm (0.0 phi size). The phi scale (Krumbein, 1934) is a negative $\log_2$ of the particle size (mm).

coral there was still a significant amount of light available, averaging 1.4% in *H. aequicostatus* and 0.6% in *H. cochlea*. The source of light could have been light penetrating through the coral from above and reaching the bottom. Indeed this was the case in the fungid coral *C. cyclolites*, where we measured 0.05% of downwelling light underneath it, but 95% of the light was extinguished when the upper part of the coral was covered with black clay (M.F., unpublished). In *H. aequicostatus*, 0.2% of the downwelling at sea floor was measured beneath the coral when it was placed on coarse sand; 46% of this light intensity still reached the center of the coral even when the whole of the coral except its bottom was covered with black clay. In contrast, only 14% of light reached its center when the clay-covered coral was placed on fine sand, corresponding to under 0.0014% of ambient light. Hence light propagation in the sand plays a major role in the availability of light to the underside of the coral and to the symbiotic dinoflagellates living there.

Light propagation is very different in the two types of sand. Reflectance from the fine sand is nearly double that of the coarse sand, and light almost does not penetrate (K, the diffuse attenuation coefficient, averaged 4600 m^{-1}, with ~1% of the light penetrating into each 1 mm). The coarse sand allowed over 10% of the light to penetrate each 1 mm ($K=\sim2200\,m^{-1}$). Similarly, scattering of the light was 30% of the light reflected from the surface being back-reflected (upwelling) at the surface of coarse sand (for practical reasons measured at 1 mm into the sand), but only 0.02% at the surface of fine sand. Measurements of side propagation of the light in the sand were limited in that light did not penetrate well into the fine sand. Hence measurements were designed so that only up to 1 mm of sand covered the sensor in the fine sand and 3–5 mm in the coarse sand. As expected, similar to the forward propagation, higher side propagation was detected in the coarse sand (2.9% of light reaching 3 mm depth) than in the fine sand (0.1% of light reaching 1 mm depth). Reflectance off the bottom of corals averaged 22% (of a white standard) in both species but showed great variability between
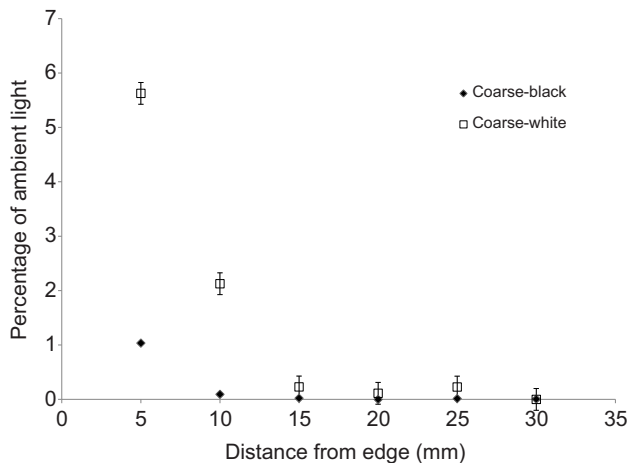
Fig. 2. Light propagation under white and black plastic placed over coarse sand. The light sources were above the aquarium to provide semi-uniform illumination, and the light sensor read light intensity in small holes along the plastic model. Light propagation in fine sand was very low (~0) under both the white and black plastic models, and hence was not plotted.
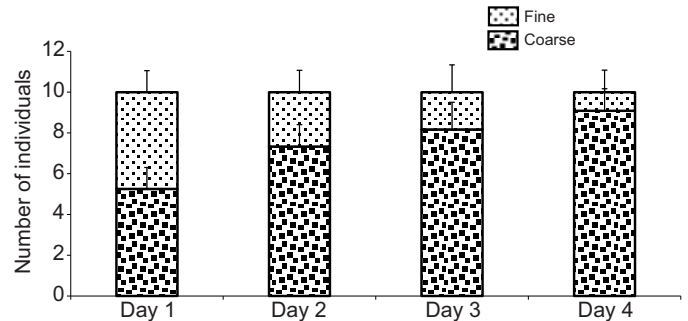

Fig. 3. Distribution of *Heterocyathus aequicostatus* and *Heteropsammia cochlea* in a tray with coarse and fine sediments. Columns represent the number of corals counted daily in each sediment type.

individual corals and even more so between different regions of the coral. In *H. aequicostatus*, dark, zooxanthellae-dense regions had reflectance of 7–15%, while regions that appeared white (low algae density) reflected more than 37% of the light. A similar trend was found in *H. cochlea*, but with a somewhat narrower range of 16–31%. It is likely that light penetrating the coarse sand will be scattered and travel under the surface because of the high scattering nature of the carbonate particles (coral, foraminifera and coralline algae skeletons) and reach the underside of the corals.

To test this, we constructed a simple plastic model (see Materials and methods). Results from this model were very much in agreement with our predictions (Fig. 2). Virtually no light penetrated beneath the model when it was placed on the fine sand (with either white or black sides facing the sand). On the coarse sand, white plastic allowed 0.2% of the light to reach up to 15 mm from the edge, with nearly 6% reaching 5 mm. A dark, black surface limited the light to 0.1% at 10 mm, and to 1% at 5 mm (light was not detectable at 15 mm). Note that our model was linear in nature, examining light arriving only from one side. Though our model illustrates well the difference in light propagation between sands, a two-dimensional study is likely to provide additional knowledge regarding light availability to the coral.

Substrate preference and phototaxis

Aspidosiphon sp. clearly preferred coarse carbonate sand over fine sand, and in the laboratory experiments carried its hosting coral to coarse sand within a few days (Fig. 3). By day 2, 70–80% of the specimens were on coarse sand and by day 4, 90–100%. This pattern repeated itself in the three runs of experiment. Each sipunculid worm dragged its coral 10–45 cm every day, allowing it to cross the border between the two substrates, a few times a day.

No phototaxis of the sipunculid could be detected. *Aspidosiphon* sp. carried its coral randomly between the light and dark areas of the experimental tray. This suggests that the sipunculid worm may not carry the hosting corals to areas that are more exposed to sunlight but rather has a preference for the substrate itself.

PAM chlorophyll fluorometry

Dark-adapted F_v/F_m values of freshly collected *H. aequicostatus* were 525±37 and 424±88 (*N*=10) for the underside and the upper side, respectively. *Heteropsammia cochlea* had mean F_v/F_m (dark adapted) values of 567±66 and 457±118 (*N*=10) for the underside and the upper side, respectively (Fig. 4). This significant difference (one-way ANOVA, *P*<0.001) suggests higher photosynthetic efficiency of the underside of these two species, probably because of acclimation to lower light intensity. Two other phototrophic cohabitants of the same environment, *C. cyclolites* and *Marginopora* sp., had a similar dark-adapted F_v/F_m values on their upper side and underside, suggesting that the two sides experience similar light intensities. Corals (*N*=7) that were grown on fine carbonate sand for 2 months lost their symbionts and/or chlorophyll on the underside of the corallite, as apparent from the transparent tissue and values of chlorophyll fluorescence (*F*) below detectable fluorescence, while corals on coarse sand (*N*=7) maintained their symbionts and had dark F_v/F_m values similar to those measured in freshly collected specimens.

DISCUSSION

Light availability to the endosymbiotic dinoflagellates located on the bottom of the corals facing the sand largely depends on two factors: the type of sand (coarse or fine) and the distance from the edge of the coral. We suggest that light reaching the coarse sand sea floor is reflected and scattered to the sides and can reach the slightly buried underside of the coral, providing light for photosynthesis by the symbiotic algae. The intensity of light within the host tissue may be over 180% greater than that of the incident light reaching the coral (Kühl et al., 1995) because of the special scattering nature of the skeleton. Photons enter the skeletal equivalent of a 'house of mirrors' (both between the substrate and coral surface and inside the coral skeleton) and bounce around for five to 10 times longer than they would if they hit a simple reflective surface. This has the direct effect of increasing the average light intensity, thereby increasing the probability of photons hitting a light-trapping pigment such as chlorophyll or another target.

High scattering of the coral surfaces causes the pathlength of light to increase greatly (Enríquez et al., 2005), as can easily be demonstrated with a typical laser pointer (Fig. 5C,D) when the laser beam is scattered, enlarging the area of illumination on the coral surface. In regions of the coral with high algal density, the light will be rapidly absorbed and will not reach the center of the coral underside because over 95% of incoming irradiance may be absorbed by the zooxanthellae (Enríquez et al., 2005). However, when the concentration of algae/chlorophyll is low or the coral bottom is fairly white (Fig. 5A), the light will be reflected back to the sand, and travel forward to a greater distance until it is absorbed by algae or by the sand (Fig. 5). This effect is even more pronounced
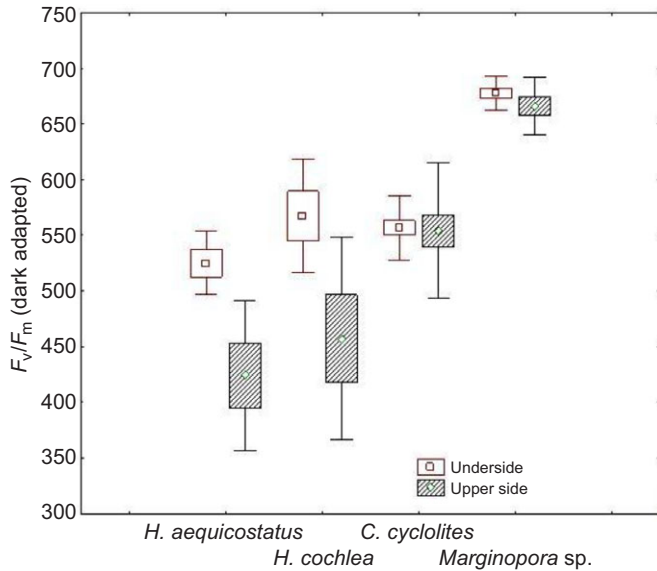
Fig. 4. Dark-adapted maximal quantum yield (F_v/F_m) of the upper side and the underside of four sand-dwelling species at the study site – the corals *Heterocyathus aequicostatus*, *Heteropsammia cochlea* and *Cycloseris cyclolites*, and the foraminiferan *Marginopora* sp. – demonstrating their light acclimation and photosynthetic capacity.

in relatively shallow water and under conditions promoting wave lensing (Nakamura and Yamasaki, 2008; Veal et al., 2010), where light intensity of wave-lencing flashes reaches 250% of mean irradiance levels. Under such conditions, light intensities hitting the substrate and reaching the underside of sand-dwelling corals may be as intense as the mean incident light reaching the upper coral

surface. It has been shown by Enríquez et al. (Enríquez et al., 2005) that corals' symbiotic dinoflagellates can be highly productive at chlorophyll densities that are five to 10 times lower than in other photosynthetic organisms, hence the underside of *H. aequicostatus* and *H. cochlea* can be bright yet photosynthetically productive. In the fine sand, however, almost all the light is reflected and absorbed and cannot reach the underside of the coral. A prerequisite for this prediction is that the surface of the coral will be mostly flat and parallel to the surface of the sand. Surprisingly, the prediction is not limited to the upper layer of the sand but will also work when the coral is partly buried in it.

Living on finer sand limits the maximal size of individuals and may limit the coral's food availability. A population of *Heterocyathus* sp. found in Eilat (Gulf of Aqaba, Red Sea) at a depth of 50 m and living on finer sand than in the GBR population was found to be composed of individuals one-third the size of GBR specimens (M.F., unpublished), possibly restricted by light availability to the underside of the coral although the water clarity was high. Similarly, specimens of this species collected in the southern Red Sea and the Indo-Pacific Ocean on muddy substrates do not fully cover the gastropod shell (Stolarski et al., 2001) and the coral has no underside. These mud-dwelling corals are rarely symbiotic and are likely to depend on heterotrophic nutrition.

Our findings suggest two different strategies of light trapping by autotrophic corals living on sand. First, *H. aequicostatus* and *H. cochlea* utilize light that scatters in the coarse carbonate sand. Light that reaches the buried areas of the coral allows an increase in photosynthesizing surface area. This, however, restricts the maximum size of these corals. The bigger the coral, the less light will reach the center of the underside. Assuming the symbiotic algae need no less than 0.1% of the downwelling light (which is amplified internally by the skeleton fine structure), one can predict that light
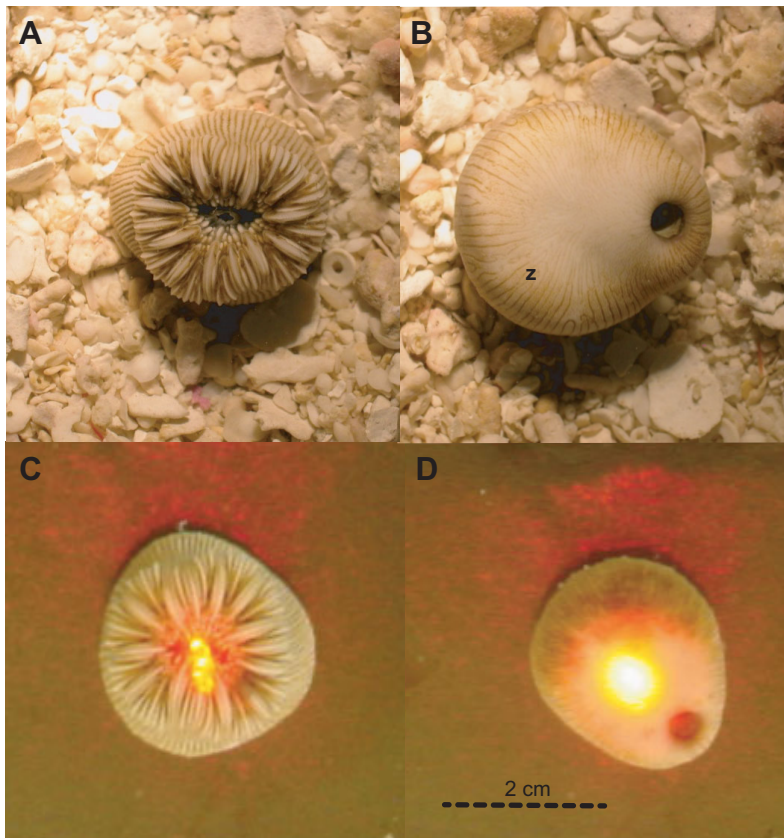

Fig. 5. Upper side (A) and underside (B) of *Heterocyathus aequicostatus*. The endosymbiotic dinoflagellates are notable on the underside of the corallite (z). When a beam from a laser pointer is used to light the upper side (C) and the underside (D) of the corallite, the scattering effect of the underside can be seen by the wider spread of the light. This scattering feature allows for light propagation under the coral.

2 cm

will reach approximately 2 cm under a white coral and ~1.2 cm under an algae-dense coral. These values correspond to the maximal radii of the corals collected. Light scattering on the underside of the coral is achieved by the special ultra-structure of the skeleton (Fig. 5). Second, semi-transparent corals such as *C. cyclolites* and *Diaseris distorta* may attain a large underside surface area and still receive enough light for photosynthesis of their underside symbiotic algae. The flat benthic *Marginopora* sp. is one of the largest (up to 50 mm in diameter) foraminiferan species, and has a relatively big hole in the middle of the cell, allowing light penetration to the underside of the cell. In this species, the F_v/F_m values of the upper side and the underside are similar, implying similar light intensities experienced by the photosynthetic symbionts on the two sides of the cell.

Reef sediments at Heron Reef are composed of over 95% calcium carbonate skeletal material, derived from the physical destruction of reef organisms (Maxwell et al., 1961). Carbonate material dislodged from Heron and Wistari Reefs may be transported to Wistari channel, where it is segregated by physical forces, mainly very strong tidal currents, into varying grain size along a depth gradient. The sipunculid warm *Aspidosiphon* sp. assists the coral in preventing burial, keeping it upright and preferentially carrying it to coarse carbonate sand (on scales of centimeters to meters). Fisk (Fisk, 1983) reported similar substrate preferences and concluded that the *Aspidosyphon* sp. actively avoids non-preferred sediments to ensure food availability and penetration of the sediment. *Aspidosiphon* sp. also anchors the coral to the substrate during strong tidal currents. By doing so, at the high densities at which these coral–sipunculid systems are found, this may have a landscaping affect, reducing movement and stabilizing the carbonate particles. Rolling of the carbonate particles prevents algal growth and organic matter accumulation, thus maintaining the white color of the carbonate particles and their optical properties. But relative stability in this unstable environment allows this community and the special symbiosis to persist.

AUTHOR CONTRIBUTIONS

M.F. wrote the paper in collaboration with N.S., S.S and O.H.G.; M.F. designed the study with N.S. and S.S.; most experiments were performed by M.F., N.S. and S.S., and O.H.-G. took part in field surveys and experiments; all authors read and commented on the manuscript.

COMPETING INTERESTS

No competing interests declared.

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