Coral Reefs
DOI 10.1007/s00338-011-0801-z

REPORT

Changes in scleractinian coral *Seriatopora hystrix* morphology and its endocellular *Symbiodinium* characteristics along a bathymetric gradient from shallow to mesophotic reef

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Received: 20 September 2010 / Accepted: 20 June 2011

Abstract The algae living endosymbiotically within coral are thought to increase algal pigmentation with increasing depth to capture the diminishing light. Here, we follow distribution of the hermatypic coral *Seriatopora hystrix* along a 60-m bathymetric gradient in the Gulf of Eilat, Red Sea, to study coral ecophysiology and response to light regimes. Combining work on coral morphology, pigment content and genotyping of the photosymbiont, we found that total chlorophyll concentration per zooxanthellae cell and the dark- and light-acclimated quantum yield of photosystem II did not vary significantly along the 60-m gradient. However, the chlorophyll a/c ratio increased with depth. This suggests that the symbiotic algae in *S. hystrix* possess a mechanism for acclimatization or adaptation that differs from previously described pathways. The accepted photoacclimatory process involves an increase in chlorophyll content per alga as light intensity decreases. Based on corallite and branch morphology, this research suggests that *S. hystrix* has two depth-dependent ecophenotypes. Above 10 m depth, *S. hystrix* exhibits sturdier colony configurations with thick branches, while below 30 m depth, colonies are characterized by thin branches and the presence of a larger polyp area. Between 10 and 30 m depth, both ecophenotypes are present, suggesting that corallite morphology may act as another axis of photoacclimation with depth.

Keywords Scleractinian coral · Symbiodinium sp. · Deep reef · Morphology · Photosynthesis · *Seriatopora hystrix* · *Chlorophyll a/c ratio*

Communicated by Biology Editor Dr. Mark Warner.

Electronic supplementary material The online version of this article (doi:10.1007/s00338-011-0801-z) contains supplementary material, which is available to authorized users.

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Introduction

The depth range of hermatypic corals (0–165 m) (Fricke and Schuhmacher 1983; Maragos and Jokiel 1986) contains an array of environmental variables including currents, temperature, water energy and light properties (Loya 1972; Huston 1985). These factors create a complex gradient with multiple interacting evolutionary pressures (Darwin 1842). Shallow-water reef systems have been widely studied, and their adaptation and acclimatization mechanisms, both ecological and biological, are well documented. However, far less research has been conducted in corals under 30 m depth, leaving significant gaps in our knowledge of deep reefs (Fricke and Schuhmacher 1983; Fricke 1996; Vermeij and Bak 2002; Vermeij et al. 2002; Lesser 2004; Mass et al. 2007).

Both light intensity and quality change dramatically with depth (Jerlov 1968; Falkowski and Raven 2007) (for the Gulf of Eilat, see Kuguru et al. 2007). The light spectrum bandwidth narrows within the water column,

Published online: 22 July 2011

reaching a wavelength peak of 465 nm (Jerlov 1968) and a bandwidth of 20 nm at the maximum depth of penetration. Light properties are one of the chief factors influencing the vertical distribution of hermatypic corals (Franzisket 1970; Falkowski et al. 1990) as they affect the photosynthetic properties of endocellular symbiotic dinoflagellates from the genus *Symbiodinium* (Masuda et al. 1993; Gattuso et al. 2006), commonly known as zooxanthellae.

In shallow, high light environments, zooxanthellae provide their host corals with most of their energy budgets (Falkowski et al. 1984). In areas with intense light and UV radiation, excess irradiance and UV may inhibit photosynthesis (Lesser 1996; Takahashi et al. 2010). Inhibition occurs via the increased production of reactive oxygen species (ROS) (Smith et al. 2005) that suppress the synthesis of proteins, particularly the D1 protein required to repair photosystem II (PSII). It has recently been suggested that yellow light (550–600 nm) along with UV is primarily responsible for photoinhibition damage, perhaps by impairing the manganese cluster in the oxygen evolving complex (OEC) (Takahashi et al. 2010). Shallow corals and zooxanthellae employ photoprotective mechanisms to minimize photodamage: examples include zooxanthellae use of non-photochemical quenchers, such as xanthophyll pigment (Venn et al. 2006); host non-fluorescent pigments (Dove et al. 2008); and host fluorescent proteins (Dove et al. 2001), widespread in photosynthetic scleractinian corals (Gruber et al. 2008) and absorptive of ROS (Bou-Abdallah et al. 2006; Palmer et al. 2009).

As the reef deepens and light attenuates, a rising concentration of chlorophylls in each photosynthetic unit (PSU) is expected to increase light absorption (Falkowski and Dubinsky 1981). Low light acclimation of dinoflagellates can also occur via an increase in the number of PSU per cell (Masuda et al. 1993). These two strategies provide the energy needed for photosynthesis (Dubinsky et al. 1984). Accessory pigments such as peridinin appear in the antennas of the PSU in constant proportion to chlorophyll a and c. They have an absorption peak at the blue and green–blue wavelengths and can also increase the amount of energy absorbed by the antennas (Iglesias-Prieto et al. 1993; Iglesias-Prieto and Trench 1997). Regardless of which approach is used, the zooxanthellae depend on increased pigmentation until it reaches an effective concentration boundary. The host coral is known to acclimate to depth by increased heterotrophy, as reported along a 60-m-depth gradient in the Gulf of Eilat (Einbinder et al. 2009) as well as on other reefs (Lesser et al. 2010). Zooxanthellae density within heterotrophically fed corals increases, even under low light conditions, and the symbionts exhibit a higher concentration of chlorophylls (Houlbreque and Ferrier-Pages 2009).

Molecular phylogeny has shown that the algae genus *Symbiodinium* can be separated into clades and subclades (Rowan and Powers 1991; LaJeunesse 2001). This division is achieved using the nuclear genes encoding ribosomal RNA (nrDNA) and within it the sequences of ribosomal internal transcribed spacers (ITS 1 and 2) (Brown et al. 2000; LaJeunesse 2001, 2003). Different clades have distinct bio-optical signatures (Hennige et al. 2009) and show depth zonation (Rowan and Knowlton 1995; Rowan et al. 1997; Toller et al. 2001; LaJeunesse et al. 2003; Iglesias-Prieto et al. 2004; Frade et al. 2008). Some coral hosts are able to associate with a variety of symbiont types (Rowan 1998; Toller et al. 2001; Sampayo et al. 2007), further, it was recently shown that *S. hystrix* and its associated *Symbiodinium* constitute genetically isolated clusters across distinct reef habitats (Bongarets et al. 2010).

Concomitantly, responses to variations in environmental conditions take place in the host. Corals show high morphological plasticity as an adaptation response to change in environmental gradients such as light, sedimentation, wave energy and flow (Bruno and Edmunds 1997). Under dim light, in both deep and shallow areas, coral colonies trend toward a wider spread, two-dimensional architecture, maximizing light harvesting and avoiding intra-colony shading (Dustan 1975; Falkowski and Dubinsky 1981; Fricke and Schuhmacher 1983; Vermeij and Bak 2002; Anthony and Hoegh-Guldberg 2003). In branching species, branches are thin and horizontally rather than subspherically arranged. Spherical species become flattened out or encrusting (Bak and Meesters 1998; Muko et al. 2000; Mass et al. 2007). Under flow variability, some corals show morphological plasticity, likely a means to increase intake of particles, dissolved inorganic carbon and gases (Sebens et al. 1997; Mass and Genin 2008) as well as dissolved organic matter (Al-Moghrabi et al. 1993). However, Helmuth et al. (1997) did not observe a morphological response to flow. Corallite morphology and spacing also vary as a response to changes in environmental conditions (Porter 1976; Bruno and Edmunds 1997; Klaus et al. 2007).

In this study, we investigate changes in zooxanthellae phylogenetic diversity, chlorophyll concentrations, chlorophyll a fluorescence and host morphology in the hermatypic coral *S. hystrix*. These changes were explored along the coral's entire bathymetric distribution range, including the deeper reef or "twilight zone." This work aimed to elucidate the patterns of acclimatization that are demonstrated by *S. hystrix*.

Seriatopora hystrix (Dana 1846), a widely distributed Indo-Pacific branching coral species, is characterized by a vast depth range (0–60 m) (Electronic Supplemental Material, ESM Fig. 1). It is a fast-growing coral, with shallow colonies reaching a diameter of 5 cm after 4 or 5 years (Shlesinger 1985). *S. hystrix* exhibits substantial colony morphological plasticity (Dai 1989) that creates a complex habitat for diverse species of crustaceans and fish,

and a variety of cryptic organisms (Dojiri 1988). In the Northern Red Sea, *S. hystrix* is common in the rear-reef and reef flat and is abundant in the fore-reef (Shlesinger 1985; Maier et al. 2005) (pers. obs, ESM Table 1).

Materials and methods

Study site

The study was conducted at a fringing coral reef on the northern tip of the Gulf of Eilat, Red Sea. The distribution of *S. hystrix* in the Gulf of Eilat is patchy; in some reefs, it is very abundant, and in others, it is non-existent (ESM Table 1). Its abundance ranges from 0.12 ± 0.02 colonies m^{-2} in the deep edges of distribution (>40 m) to 0.78 ± 0.29 colonies m^{-2} on the reef flat in the shallow edge of distribution, to 2.57 ± 0.11 colonies m^{-2} in the coral's center of distribution (20–28 m). Hence, the coral's abundance creates a bell-shaped curve (ESM Fig. 1). Data on abundance and distribution were collected using a series of line transects run underwater, each 10 m in length, comparable to the method described by Loya (1972).

Three sites were studied throughout 2005: Dekel Beach, "DB" (N 29 31.357, E 34 56.070); Japanese Gardens, "JG" (N 29 30.296, E 34 55.176); and the oil terminal "KATZA" (N 29 31.357, E 34 56.070) (World Geodetic System 84 reference frame). These sites were surveyed as described above to 90 m depth without discovery of *S. hystrix* lower than 60 m. The KATZA location was surveyed and served as a reference site because of its prohibition on commercial diving activity. The distribution of colony phenotypes at KATZA was recorded, but fragments were not collected. Light measurement data of photosynthetic active radiation (PAR) in the study sites were taken from the work of Kuguru et al. (2007).

Orientation of colonies toward downwelling light

In each of the study sites, three randomly positioned transects were established perpendicular to the shoreline, to a depth of 60 m. The depth of every fifth colony was measured along the transect, and its position toward downwelling light was established. Each colony's exposure to ambient light was described according to the following four categories: growing upward and not shaded; growing sidewise and not shaded; growing upward and shaded; and growing sidewise and shaded.

Sample collection

Fragments were collected every 10 m along the reef slope from two sites: JG (at depths 0.1 and 10 m) and DB (at depths 20, 30, 40 and 50 m). At the deepest edge of distribution, very few colonies were found, and fragments were therefore collected only to 50 m. At each depth, five 5-cm fragments were collected from five different colonies. To attain a well-distributed sample set, the corals were sampled at least 2 m apart from each other. In order to achieve uniform light conditions for all fragments collected, the colonies chosen were facing upwards and not shaded. Moreover, all fragments were collected from the uppermost portion of the colony facing direct downwelling irradiance. Fragments were used for the determination of corallite size and spacing, and branch thickness, algae number, chlorophyll concentration and algal phylogeny.

Fragment handling and analysis

Fragments from the reef were removed and placed in running seawater tables. Shallow fragments (0.1 and 10 m) were exposed to 60% surface light intensity and deep fragments (20–60) to 2.5% surface light intensity. Filtering levels correspond to light intensity measured in the Gulf of Eilat at depths of 8 and 50 m (840 and 35μE at midday), respectively. Care was taken to prevent exposure of deep fragments to levels beyond 2.5% surface intensity. Tissue was removed from all fragments by airbrush within 3 h of collection and placed into 15–25 ml filtered seawater. The tissue was then analyzed for algae count using a C-Chip™ hemocytometer (Falkowski and Dubinsky 1981), and chlorophyll measurement was taken as follows: the slurry was filtered through Whatman GF/C (1.2 μm), filters and chlorophyll a and c were extracted in cold acetone (90%) overnight at 4°C. Chl a and c concentrations were determined spectrophotometrically according to the equations of Jeffrey and Humphrey (1975), using an Ultraspec 2001 Pro (Biochrom) spectrophotometer. Samples were normalized to the number of algae cells. Simultaneously, zooxanthellae DNA was extracted and skeletons submerged in bleach to remove residual tissue before morphological measurements.

Data analysis was conducted using Statistica 7 software (StatSoft). When analysis of variance test (ANOVA) was used, assumptions regarding homogeneity of variance were first met in Levene's test.

Morphology analysis

Corallite size and spacing and branch thickness were measured on bleached skeleton fragments (top 5 cm of the branch). Skeletons were observed and measured using a WILD M5A binocular (Wild Heerbrugg). All measurements were taken 2–3 cm from the tip of the fragment, and five parameters were measured: diameter of branch (measured with a caliper), diameter of corallite, distance between rows of corallites, distance between corallites in a

row and number of corallites (i.e., of polyps, for the last three parameters). Corallites in *S. hystrix* are neatly arranged in clear rows, hence its name (*Seriatopora* means *serial*). Three replicates per fragment were measured and averaged to a single value. One researcher performed all measurements to reduce variability and error. Measured parameters were normalized to surface area, calculated using the wax paraffin method (Stimson and Kinzie 1991), with the final surface area the average of three measurements. From these data, the surface area of corallites was calculated out of the polypary surface area:

$$\frac{\text{number\_of\_corallite\_} * \text{ave. coralliteradius } \mu\text{m}^2 * \pi}{\text{branch\_surface\_area } \mu\text{m}^2}$$

and the number of corallites per surface area:

$$\frac{\text{number\_of\_corallite}}{\text{Branch\_Surface\_Area } \mu\text{m}^2}.$$

Multivariate analysis was conducted on these intra-colony measurements. A principal component analysis (PCA) and analysis of similarity (ANOSIM) were carried out using the correlation matrix (i.e., standardized data). The software PRIMER (Plymouth marine laboratory) was used to investigate multivariate associations among the morphological traits and the nature of the multivariate differences between depth groups.

Colony morphology was surveyed along the previously described transects. Length, width and height were measured for every fifth colony along the transect, where *Length* is the longer axis of the colony surface, *Width* is the shorter axis of colony surface, and *Height* is the highest point of the colony to the substrate. Colony size is described as averaged diameter of the length and width (Edmunds 2005); the flattening of the colony is assessed according to its height. These parameters refer only to colony parts covered with living tissue.

DNA extraction of zooxanthellae and ITS amplification

Airbrush slurry was centrifuged at 5,000*g* for 5 min at 4°C. The pellet was suspended in 600 µl 2XCTAB (0.1 M Tris, 14 M NaCl, 0.02 M EDTA, 2% CTAB). Proteinase K was added to a final concentration of 20 mg ml^{-1} (BioLab). Ependofs were incubated for 1 h at 65°C, followed by one Phenol CIA extraction (Phenol: Chloroform:Isoamyl alcohol, 25:24:1) and one CIA extraction (Chloroform:Isoamyl alcohol, 24:1). The crude DNA was recovered by precipitation for 1 h in 1 ml 95% EtOH at −70°C. After centrifugation, the pellet was washed twice with 70% EtOH and dried in a 65°C oven for 1 h. The DNA was dissolved in 50 µl of double distilled water (DDW).

The ITS1- 5.8S- ITS2 rDNA regions were amplified together by polymerase chain reaction (PCR). A final reaction volume of 70 µl contained 35 µl PCR master mix (ABgene) (50% of final volume) with Thermoprime Plus DNA Polymerase. Forward primer cola and reverse primer colb (Coleman et al. 1994) (matabion) were added to a final concentration of 0.5 µM each. Three microliters of DNA and DDW was added to complete the volume. Amplification was carried out on an Advanced Primus 96 (Peqlab) with the following steps: the cover was heated to 110°C, one cycle at 95°C for 5 min followed by 30 cycles at 95°C for 30 s, 50°C for 1 min and 72°C for 1 min. Final elongation was for 5 min at 72°C. The reaction product was about 600 bp. Amplifications were checked for length, purity and yield on ethidium-bromide-stained 1.5% TAE agarose gels according to standard methods. The PCR fragments were purified using the Qiaquick Gel Extraction Kit (Qiagen) according to manufacturer's protocol.

Sequencing and analyses

Direct sequencing was performed on PCR products by HyLabs (Israel). Reagents and reaction conditions for sequencing were supplied and specified by ABI Prism Big Dye Terminator v.1.1 Cycle Sequencing Ready Reaction Kit (PE Applied Biosystems). Reaction products were analyzed on an applied 3700 Genetic Analyzer (ABI). Sequences of ITS1 and ITS2 regions (223 and 210 bp, respectively) were viewed and evaluated using Chromas 2.13. Phylogenetic analysis was conducted on aligned data using ClustalW (BioEdit software package version 5.0.6). Sequences were blasted to sequences acquired from GeneBank: AF411414, AF411413, AB207196, AB190269, SSP278598, AF334659, AF360578, AF333505, AF333511, AF333517, AB190269. These sequences were used to delineate the boundaries of the ITS1 and ITS2 regions.

Chlorophyll fluorescence measurements

Samples were collected from the shallowest *S. hystrix* colonies on the reef flat and from a depth of 60 m. Three colonies were sampled from each depth; one fragment per colony. Fragments were placed in running seawater tables, shallow fragments were exposed to 90%, and deep fragments were exposed to 2.5% of surface light (about 1,260 and 35 µE, respectively, on midday of the experiment). Care was taken not to expose deep fragments to any high light. Fragments were experimented upon within 3 h of collection. Chlorophyll fluorescence parameters were measured using a dual pulse amplitude modulated fluorimeter (Dual PAM-100, Heinz Walz GmbH) on algae within the tissues (*in hospite*) of coral branches held in seawater. The samples were dark adapted for a period of 20 min before measurement (Jones and Hoegh-Guldberg 2001). The initial fluorescence (F_0) was measured using

3-μs pulses of a light emitting diode (LED, peak emission at 635 nm). A saturating pulse (10,000 μmol quanta m^{-2} s^{-1} PAR, 200 ms pulse width) was then applied to give the maximal fluorescence value (F_m). Ambient red light was thereafter switched on (LED, peak emission at 635 nm), and maximal fluorescence was measured continuously while increasing light intensity as follows: 13, 60,173, 538 and 1,294 μmol quanta m^{-2} s^{-1}. Exposure time for each light step was 5–10 min, until the F_m and F_0 signals reached a steady state. Then, ambient light was switched off and dark relaxation was measured continuously for 10 min. The ratios of variable fluorescence after dark acclimation (F_v, where $F_v = F_m - F_o$) to F_m and during illumination in ambient light $F'_q/F'_m = (F'_m - F)/F'_m$ were calculated (Genty et al. 1989). For a comprehensive review of chlorophyll fluorescence terminology, see Cosgrove and Borowitzka (2011).

Results

The effect of depth on the exposure of colonies to downwelling irradiance

Seriatopora hystrix colonies exposed to maximum downwelling light increased with depth, from 20% of the colonies between 1 and 10 m to 100% at 40–60 m. At 0–10 m, almost 50% of colonies were hidden, while in contrast at 40–60 m, there were no hidden colonies. These changes were gradual (Fig. 1). Colonies' colors were coded by colorwheel. Colors varied with depth as follows: shallow colonies (top 5 m) appeared light yellow; 10–30 m colonies were light blue or light pink; below 30 m, all colonies appeared dark brown.

The effect of depth on morphology

Colony size, measured by average diameter, and flatness, assessed by colony height, did not change significantly along depth distribution (linear regression: $n = 244$ colonies, $r^2 = 0.001, 0.01$, $P = 0.82, 0.05$, respectively) (Fig. 2).

Corallite size ranges between 545 ± 77 μm in the shallower 0.1–20 m, to 649 ± 54 μm in the deeper 30–50 m of distribution (mean ± SD). Spacing and branch thickness changes across depth were examined using PCA ordination (Fig. 3, Table 1). The principal component of the ordination (PC1) explained 34.3% of the multivariate variance and was characterized by high positive loadings of surface area and corallite number (see Table 1). This axis separated the shallow colonies from those at 30, 40 and 50 m. One-way ANOVA between these depths on PC1 scores showed a significant difference ($n = 5$, $F_{3,16} = 9.53$, $df = 3$, $P < 0.01$; post hoc showed differences between shallow and 30-, 40- and 50-m depth colonies, $P < 0.01$). PC2 explained 23.5% of the variance and is characterized by high positive loadings of row spacing and high negative loadings of branch

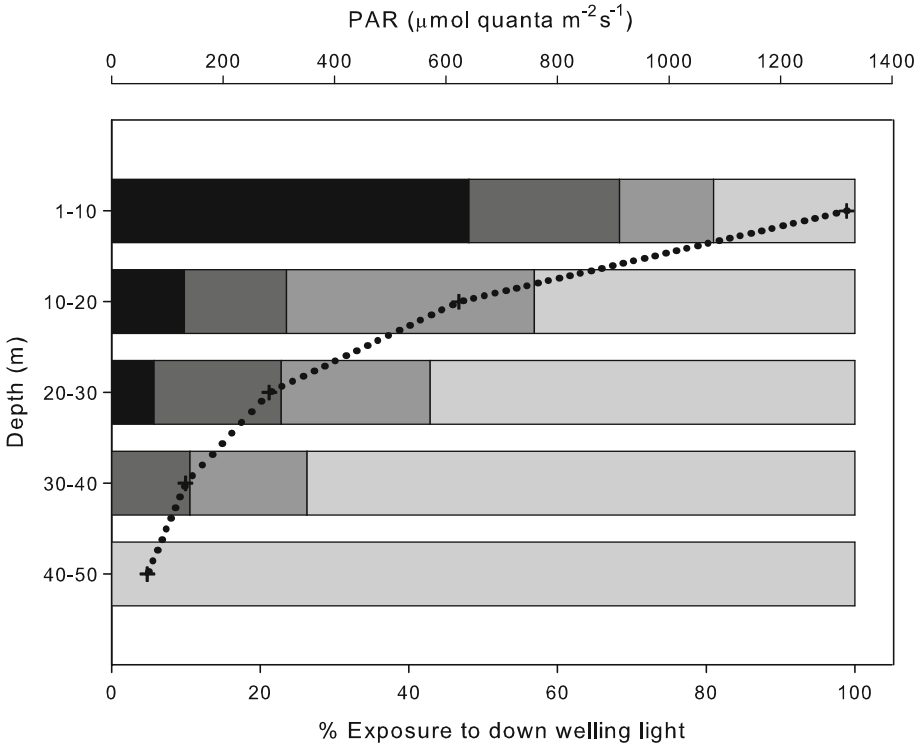

Fig. 1 The effect of depth on *Seriatopora hystrix* colony position toward downwelling irradiance. Relative exposure is conveyed by a four-color range from *light gray* representing maximum light flux, to *black* indicating *shaded colonies* (growing upward and not *shaded*, growing sidewise and not *shaded*, growing upward and *shaded*, growing sidewise and *shaded*). *Dotted line* indicates average photosynthetically active radiation during 2005. $N = 258$ colonies

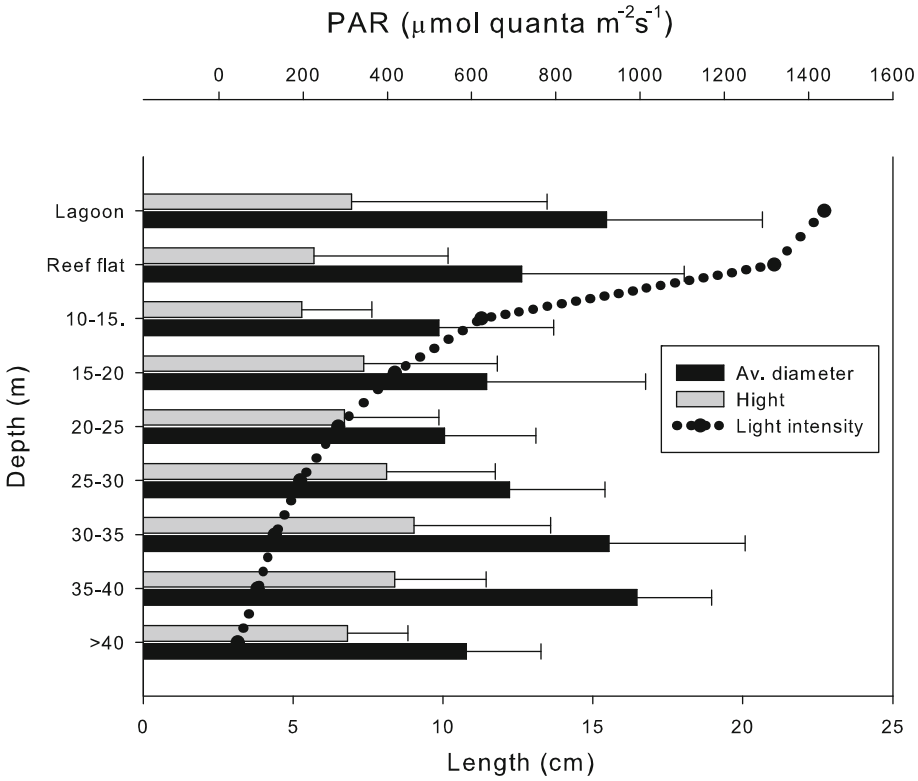

Fig. 2 The effect of depth on *Seriatopora hystrix* colony size and height. Mean and standard deviations are presented. *X* axis represents length of diameter or height in cm. *Dotted line* indicates average photosynthetically active radiation in 2005. $N = 244$ colonies

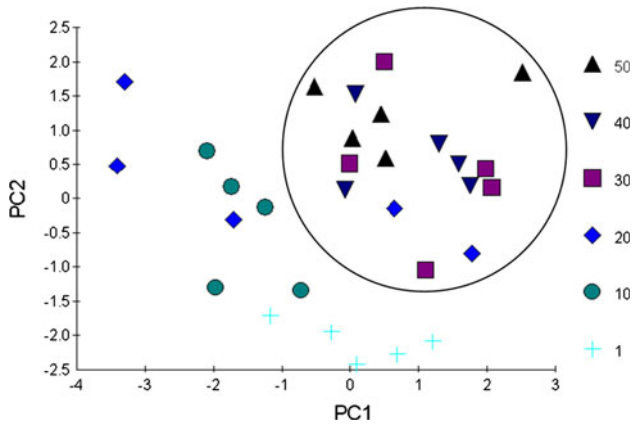

Fig. 3 Principal component analysis ordination, performed on morphological colony attributes. The first two component axes are presented (PC1, PC2). Five fragments of each depth (1, 10, 20, 30, 40 and 50 m) are represented by *five colors*. The *circle* circumscribes deep colonies: 30, 40, 50 m, and two colonies from 20 m. Colonies from 1 m are separated from other depths on PC2 (Eigenvalues presented in Table 1, significance of difference in Table 2, results of ANOSIM). $N = 5$ fragments at each depth

diameter. The separation between the reef flat and other depths occurred on this axis. One-way ANOVA between all depths on PC2 scores showed significant variance ($n = 5$, $F_{5,24} = 11.08$, $df = 5$, $P < 0.001$; post hoc showed differences between 1 m and all other depths, $P < 0.01$).

Pair-wise ANOSIM confirmed groupings suggested by the PCA (Table 2) as no significant difference in intra-colony morphology was found between the deep populations (30, 40, 50 m). However, significant differences exist between deep and shallow populations (30–50 m vs. 1–10 m) and between populations at 1 and 10 m.

Based on these analyses, two distinct depth-dependant phenotypes were found. The shallow ecophenotypes are characterized by thick branches, short and wide colonies and dense corallite rows in tandem with small total corallite surface area. In contrast, the deep ecophenotypes have slender branches, taller and slimmer colonies and greater total corallite surface area relative to the shallow type.

The effect of depth on zooxanthellae

Zooxanthellae density increases at the deepest edge of distribution, from $6.4 \times 10^5 \pm 1.2 \times 10^5$ cells*cm^{-2} at 40 m to $9.9 \times 10^5 \pm 3.3 \times 10^5$ (mean ± SE) at 50 m (one-way ANOVA, $n = 5$, $F_{4,20} = 6.66$, $P < 0.01$, post hoc Tukey performed on ANOVA revealed $P = 0.053$ between 50 m and other depths) (data not shown). Chl a and c concentrations per alga doubled from shallow to intermediate depth. The values varied from 0.73 ± 0.23 and 0.97 ± 0.44 (mean ± SE) pg Chl zooxanthellae^{-1} in the shallow depth (on the reef flat) to 1.61 ± 0.87 and 2.74 ± 1.98 (mean ± SE) pg Chl zooxanthellae^{-1} at

Table 1 Principal component analysis ordination of 6 morphological attributes, from fragments collected every 10 m along a depth gradient (0.1, 10, 20, 30, 40, 50 m depth)

Parameter	PC 1	PC 2	PC 3	PC 4	PC 5
Eigenvalues	2.40	1.64	1.39	0.79	0.45
Explained variance	34.3	23.5	19.9	11.2	6.4
Component loadings					
Corallite number* cm^{-2}	0.554	0.027	0.201	−0.153	−0.638
Branch diameter mm	−0.187	−0.556	−0.411	−0.088	−0.356
Between row spacing	−0.124	0.315	−0.444	−0.809	−0.021
Spacing in row	0.030	0.715	0.020	0.107	−0.033
Corallite diameter	0.428	−0.049	−0.542	0.190	0.501
Corallite area* cm^{-2}	0.611	0.001	−0.251	0.054	−0.100

The first two component axes are represented in Fig. 3. Between row spacing = average distance between rows of corallites. Spacing in row = average spacing between corallites in a single row. $n = 5$ fragments at each depth

Table 2 Results of analysis of similarity (ANOSIM) for morphological similarities between all depths

Depth (m)	Pair-wise R statistic	Significance level (*P* value)
50 versus 40	−0.044	0.556
50 versus 30	0.176	0.135
50 versus 20	0.18	0.127
50 versus 10	0.568	*0.008
50 versus 1	0.804	*0.008
40 versus 30	−0.06	0.73
40 versus 20	0.156	0.143
40 versus 10	0.732	*0.008
40 versus 1	0.848	*0.008
30 versus 20	0.176	0.151
30 versus 10	0.776	*0.008
30 versus 1	0.62	*0.008
20 versus 10	0.092	0.206
20 versus 1	0.428	0.016
10 versus 1	0.752	*0.008

Test statistics and significance level (*P* value) are presented. Values marked with * indicate significant dissimilarity between depths at the 0.05 level. $n = 5$ fragments at each depth

20 m. These concentrations remained constant to a depth of 50 m (Mann–Whitney was performed between each sequential depth, between 1 and 20 m; chl a: $Z = -1.98$, $P = 0.04$; chl c: $Z = -1.98$, $P = 0.047$; no significant difference between other sequential depths) (Fig. 4). The Chl a/c ratio doubled from 0.64 ± 0.23 at 20- m to 1.25 ± 0.2 (mean ± SE) at 50 m (Fig. 4). One-way ANOVA showed significant differences between depths ($n = 5$, $F_{4,20} = 7.05$, $P < 0.01$); post hoc Tukey showed significant differences between 50 m and all other depths ($P < 0.05$). *Fv/Fm* did not differ significantly between shallow 1 m coral and deep 60 m coral for the following treatments (values represent 1 and 60 m groups, respectively, mean ± SD): dark acclimation [$Fv/Fm = 0.69 \pm 0.007$, 0.7 ± 0.02], light intensities of 60 µmol quanta cm^{-2} s^{-1} [$Fq'/Fm' = 0.63 \pm 0.006$, 0.61 ± 0.03], light intensities of 173 µmol quanta cm^{-2} s^{-1} [$Fq'/Fm' = 0.57 \pm 0.05$, 0.53 ± 0.04], 538 µmol quanta cm^{-2} s^{-1} [$Fq'/Fm' = 0.4 \pm 0.1$, 0.36 ± 0.07], 1,294 µmol quanta cm^{-2} s^{-1} [$Fq'/Fm' = 0.24 \pm 0.08$, 0.26 ± 0.12] and dark relaxation [$Fq'/Fm' = 0.5 \pm 0.04$, 0.5 ± 0.03] (Fig. 5).

Effect of depth on zooxanthellae phylogeny

The taxonomic affiliation of the symbiotic algae at the level of clades or subclades remained constant along the depth gradient. All *Symbiodinium* sp. tested in this study belong to clade C and show the greatest similarity to type C3nt, as reported by Sampayo et al. (2009). Representative sequences are available on GeneBank (Table 3). More than one zooxanthellae taxa has been reported in a colony, following internal gradients of environmental irradiance (Rowan and Knowlton 1995; Rowan et al. 1997). This was also found in *S. hystrix* (Sampayo et al. 2007). Therefore, it is plausible that the corals we sampled contain more than one taxa of zooxanthellae.

Discussion and conclusions

The holobiont

A behavioral response of the holobiont to irradiance quality/quantity determines colony orientation toward or away from downwelling light (Dustan 1982; Gleason and Wellington 1995; Gleason et al. 2006; Frade et al. 2008). The reciprocal ratio between light intensity and coral exposure is presented in Fig. 1. Light intensity at 40–60 m

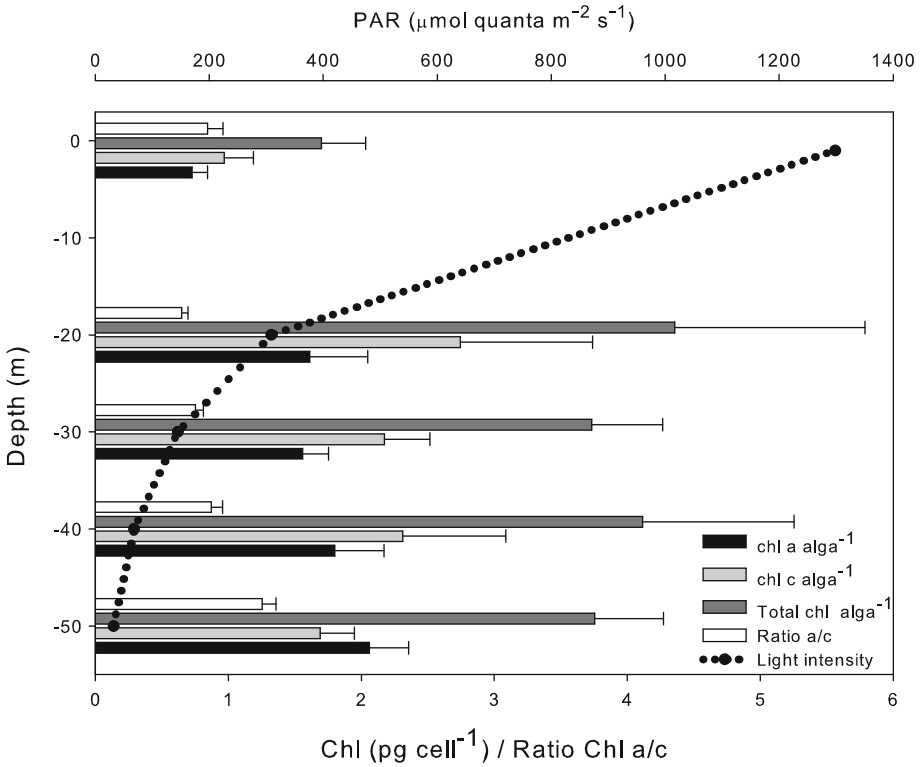

Fig. 4 The effect of depth on concentration of photosynthetic pigments Chlorophyll a, Chlorophyll c, total Chlorophyll and Chlorophyll a/c ratio, per algal cell. Mean and standard deviations are presented. *Dotted line* indicates photosynthetically active radiation during the month the fragments were collected. There is an increase in the concentration of Chl a, Chl c and total Chl between 1 and 20 m depth. $N = 5$ fragments at each depth

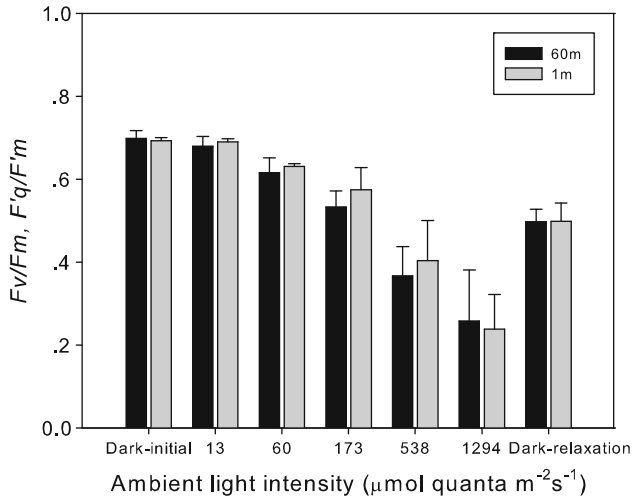

Fig. 5 *Fv/Fm* and Fq'/Fm' under different light intensities. Corals were collected from 60 m (*black*) and 1 m (*gray*). *Bars* indicate standard deviation. No significant difference was found between depths. $N = 3$ fragments at each depth

Table 3 GeneBank submission numbers of ITS 1 and ITS 2 reprehensive sequences from a depth range of 0.1–50 m

Submission Num. in GeneBank	Depth	Sequence
FJ599703	Lagoon	ITS1
FJ599704	20 m	ITS1
FJ599705	20 m	ITS1
FJ599706	40 m	ITS1
FJ599707	50 m	ITS1
FJ599708	Lagoon	ITS2
FJ599709	10 m	ITS2
FJ599710	30 m	ITS2
FJ599711	50 m	ITS2

varies throughout the year between 3 and 120 µmol quanta m^{-2} s^{-1} in the Gulf of Eilat (Kuguru et al. 2007), and, at this depth, there are no shaded colonies. Furthermore, there is no record of *S. hystrix* below 60 m in the Gulf of Eilat. It is apparent that *S. hystrix* cannot survive under extremely low light regimes. In shallow areas, only 20% of the colonies are exposed to the maximal downwelling light, corresponding to 875–1,408 µmol quanta m^{-2} s^{-1} in the first meter of the water column (Fig. 1). The 0- to 30-m colonies are mainly yellow, light blue and pink, representing pigments that can inhibit photodamage (Dove et al. 2001, 2008; Takahashi et al. 2010).

The distribution can be explained by a mechanism of settlement cues (Koehl and Hadfield 2004), i.e., light quality/quantity directly influencing planulae localization within the reef. Thus, a planula will settle when it senses that it is physically, photosynthetically and biochemically adapted (Lewis 1974; Gleason and Wellington 1995; Gleason et al. 2006).

The zooxanthellae

Seriatopora hystrix's zooxanthellae acclimation to low light at depths 0–20 m corresponds with an accepted mechanism suggesting that the amount of photosynthetic pigments per algal cell increases as light intensity decreases. The number of photosynthetic units per cell remains stable, but the size of the light-harvesting complex units (LHC) per reaction center increases (Falkowski and Dubinsky 1981; Kinzie et al. 1984; Porter et al. 1984; Wyman et al. 1987; Kuguru et al. 2007). The latter increases the relative absorption cross-section for photosystem II (PS II); thus, the electron-transfer rate from PSII reaction centers to the primary electron acceptor (Q_A) is optimized even under lower light levels. A second low-light pathway suggests that acclimation occurs via an increase in the number of PSU per zooxanthellae cell (Masuda et al. 1993; Iglesias-Prieto and Trench 1997), similarly increasing the relative PS II absorption cross-section. In both mechanisms, pigment density (mainly Chl a and c concentrations) is expected to increase per cell of algae with light attenuation; *Symbiodinium sp*. may acclimate by a combination of both pathways.

However, in this research, the chlorophyll content per cell (both a and c) below 20 m depth remained stable (Fig. 4), in spite of a tenfold decrease in light intensity between 20 and 50 m depths. The fact that no increase in antenna size (i.e., no increase in total chlorophyll) was found is not surprising since it can reach an effective limit (Falkowski and Laroche 1991); the same argument applies to PSU at depth. A similar pattern of chl a change over a depth gradient was reported from deep-dwelling *Stylophora pistilata* (down to 55 m) (Mass et al. 2007).

Fv/Fm in a dark-adapted sample is proportional to the fraction of reaction centers capable of converting absorbed light to photochemical energy (Kraus and Weis 1991). The ratio is a convenient measure of the maximum potential quantum yield. Accordingly, Fq'/Fm' represents the effective quantum yield of PS II (Genty et al. 1989). Both ratios did not change between depths, although the high light intensity used, 1,294 µmol quanta cm^{-2} s^{-1}, is an order of magnitude higher than the maximum light intensity found at 60 m depth. This result may indicate that the number of PS II reaction centers is similar between depths. In contrast to our results, Jones and Hoegh-Guldberg (2001) compared high and low light-adapted *Montipora digitata* and *Stylophora pistillata* colonies (versus shallow and deep), showing that upon high illumination *Fv/Fm* dropped markedly in shade corals compared to the light-adapted group.

The interesting phenomenon of an upshift in the a/c chlorophyll ratio with increasing depth (Fig. 4) contrasts with previous coral studies (Dustan 1982), as well as findings that higher plants and green algae downshift chlorophyll a/b ratios under lower light conditions. In plants, a lower chl a/b ratio indicates that more energy is efficiently transferred to PS I via light-harvesting antenna complexes (Melis and Harvey 1981; Leong and Anderson 1984; Torre and Burkey 1990; Melis 1991; Yamazaki 2010). Several groups have noted the presence of chl c2 in direct association with PSI, either within the reaction center (Prezelin 1987, Iglesias-Prieto et al. 1993) or demonstrated by the presence of chlorophyll a/c binding proteins with PS I (Janssen and Rhiel 2008). Therefore, a change in the chl a/c ratio may indicate a change in the ratio of PS I to PS II. These contradicting physiological results may be because most of the published zooxanthellae acclimatization data was derived from comparisons between high and low light-adapted zooxanthellae without regard to light quality (band width). In deep reef corals, changes in light intensity and quality may greatly influence the amount of energy absorbed by both PS I and PS II.

The genotype of the symbiotic algae found in *S. hystrix* most resembles symbiont type C3nt, found in the Great Barrier Reef. *S. hystrix* has been known to exhibit a single symbiont type at a given location, along a depth gradient of 3–19 m (Loh et al. 2001; Sampayo et al. 2007, 2009). Another study has also shown that type C3nt inhibits *S. hystrix* at 30 m, while shallow corals are inhibited by other types (Bongarets et al. 2010). The resolution of this phylogenetic analysis will not allow us to determine whether the observed adjustment of zooxanthellae to deep water conditions is through adaptation or acclimatization.

It is known that deeper corals rely more on predation (Dodge et al. 1974; Tomascik and Sander 1985; Steen 1986; Muscatine et al. 1989; Anthony and Fabricius 2000; Palardy et al. 2006; Einbinder et al. 2009). Increased corallite areas found for deeper *S. hystrix* (30, 40, 50 m) (Fig. 3) may indicate the same applies in the Gulf of Eilat.

Two possible pathways presented below may explain the adjustment in *S. hystrix* to the variation in light quality and quantity with depth. It is possible that photosynthetic efficiency decreases in the deep reef, causing the coral to switch to a greater reliance on predation (Muscatine et al. 1989). Alternatively, the coral changes its PS I to PS II ratio. The latter strategy may be combined with enhanced light trapping in the skeleton (Enriquez et al. 2005).

The effect of depth on colony morphology

As light intensity decreases with depth, coral colonies tend to flatten and branches become more spacious. These changes are believed to increase the amount of light that can be utilized by the symbiotic algae (Graus and Macintyre 1976; Fricke and Schuhmacher 1983; Bruno and Edmunds 1997; Muko et al. 2000; Anthony and Hoegh-

Guldberg 2003). Wave energy and currents also affect coral morphology (Dai 1989; Mass and Genin 2008). Mass flux to coral tissue was correlated to increased colony surface area and changes in morphology (Fabricius et al. 1995; Helmuth et al. 1997, Sebens et al. 1997); however, strong waves and currents prevail only at the top 30 m of the water column in the narrow Gulf of Eilat.

Seriatopora hystrix's size and height were unaffected by the diminishing light along the depth gradient (Fig. 2). Thus, self-shading further decreases the amount of light available to the symbiotic algae.

Perhaps changes in parameters such as corallite size and spacing and branch diameter enable colonies to cope with extreme light conditions. It appears that two distinct ecophenotypes exist (Fig. 3)—*deep* (30–50 m) and *shallow* (0–10 m)—and that the transition zone between the types occurs at 20 m where colonies can assume both deep and shallow phenotypes. These data accord with total chlorophyll, which reaches a peak at 20 m and remains stable until 50 m (Fig. 4).

In the shallow areas of distribution, the reef-flat colonies have a sturdier configuration with thick branches. The reef flat is distinguished from deeper parts of the reef by its extremely high photon flux density and stronger water energy, including wave, tidal forcing and flow (Storlazzi et al. 2005). Both factors can affect coral morphology (Bruno and Edmunds 1997; Mass and Genin 2008), and it is thus impossible to attribute entire morphological change to one factor; however, thick branches can reduce the amount of damage caused by wave action (Marshall 2000). Reciprocal transplantations should be conducted to determine whether these two ecomorphotypes are adaptive or emerged via acclimatization response of a high-plasticity coral species.

Contrary to current dogma, we demonstrate that the chlorophyll concentration per zooxanthellae cell was relatively stable along the entire depth gradient, and chlorophyll a/c ratio increased with depth. In addition, one algae genotype was found to occupy the entire depth gradient, indicating photoacclimation of the algae. Therefore, we suggest that *S. hystrix* possesses an acclimation mechanism that differs from any previously described pathway. This study emphasizes the need to further explore the deeper, mesophotic portions of coral reefs and the novel physiological mechanisms present in this relatively unexamined "twilight zone."

Acknowledgments We thank K. Zendbank for assisting in molecular work and the Interuniversity Institute for Marine Sciences and staff in Eilat, Israel, for contributing to field studies. We also thank M. Kiflawi and B. Goodman-Tchernov for their shared insight and E. Brokovitch for participating in the technical dives. The research was supported by the Israeli Science Foundation grant # 981/05, the Bundesministerium für Bildung und Forschung, Germany, grant # 1923–1300 and the US National Science Foundation grant # 0920572.

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