



Mesophotic coral depth acclimatization is a function of host-specific symbiont physiology

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Mesophotic coral ecosystems receive increasing attention owing to their potential as deep coral refuges in times of global environmental change. Here, the mechanisms of coral holobiont photoacclimatization over a 60 m depth gradient in the central Red Sea were examined for the four coral genera *Porites*, *Leptoseris*, *Pachyseris*, and *Podabacia*. General acclimatization strategies were common to all host-symbiont combinations, e.g., *Symbiodinium* cell densities and photoprotective (PP) to light-harvesting pigment ratios both significantly decreased with water depth. *Porites* harbored *Symbiodinium* type C15 over the whole 60 m depth range, while *Pachyseris* and *Podabacia* had limited vertical distributions and hosted mainly *Symbiodinium* type C1. *Symbiodinium* type C15 had generally higher xanthophyll de-epoxidation rates and lower maximum quantum yields than C1, and also exhibited a strong photoacclimatory signal over depth that relates to the large distribution range of *Porites*. Interestingly, the coral host had an effect on *Symbiodinium* pigment composition. When comparing *Symbiodinium* type C1 in *Podabacia* and *Pachyseris*, the β -carotene chl a^{-1} , the peridinin chl a^{-1} , and diadinoxanthin chl a^{-1} ratios were significantly different between host species. Our data support a view that depth acclimatization of corals in the mesophotics is facilitated by *Symbiodinium* physiology, which in turn is host-specific.

Keywords: coral reef, mesophotic coral, Red Sea, *Symbiodinium*, photosynthetic pigments

INTRODUCTION

Light in the ocean decreases exponentially with depth and it is one of the most important factors shaping coral communities (Falkowski and Dubinsky, 1981; Dubinsky et al., 1984). Below 30 m depth, mesophotic coral communities act as an extension of shallow water reefs until the bottom of the photic zone (Kahng et al., 2010). While light limitations constraint most *Symbiodinium*-bearing corals to depths shallower than 90 m, photosynthetically active corals can be found as deep as 145 m in the Red Sea owing to the transparency of the water column (Schlichter et al., 1986). This is because corals rely on light energy for the photoautotrophic carbon production through their dinoflagellate endosymbionts from the genus *Symbiodinium* (Muscatine and Porter, 1977; Muscatine et al., 1981).

In *Symbiodinium*, light-harvesting (LH) and photoprotective (PP) pigments form part of the photosynthetic apparatus. The major LH pigments are chlorophyll *a* (chl *a*), chlorophyll *c*₂ (chl *c*₂), and peridinin (per) that build different protein complexes to harvest available light energy (Iglesias-Prieto and Trench, 1997). Diadinoxanthin (ddx) and diatoxanthin (dtx) are components of the xanthophyll cycle in dinoflagellates, and together with β -carotene (β -car) comprise the PP pigments (Jeffrey and Haxo, 1968; Brown et al., 1999). β -carotene is found in both photosystems together with chl *a* where it mainly acts as a sink for excess light energy, but also aids in stabilizing the photosystem

structure (Kirk, 1994; Frank and Cogdell, 1996; Fromme et al., 2006).

To optimize production rates at differing irradiances, *Symbiodinium* undergo photoacclimatization of their pigment components. With decreasing light, *Symbiodinium* harbor more LH pigments, while PP pigment concentrations decrease (Falkowski and Dubinsky, 1981; Dubinsky and Stambler, 2009). The enrichment of LH pigments leads to two potentially co-occurring photoacclimatization processes, namely increases in size and number of photosynthetic units (PSU) (Falkowski and Owens, 1980; Falkowski and Dubinsky, 1981). However, this relationship is not linear as self-shading of light harvesting units eventually leads to decreased photosynthetic efficiency (McCloskey and Muscatine, 1984). Further depth acclimatizations include an increase in photosynthetic efficiency in deeper water (Lesser et al., 2010) and maximum photosynthetic rates at lower irradiances (Falkowski et al., 1990).

Generalist coral species with wide bathymetric distributions, e.g., *Stylophora pistillata* and *Seriatopora hystrix*, change their colony morphology in deeper water toward flat shapes with thinner, wider spreading branches in order to decrease self-shading and maximize light capture (Einbinder et al., 2009; Nir et al., 2011). The spacing and size of polyps might also be adjusted, as light exposure is higher in corallites than in coenosarcs tissues (Wangpraseurt et al., 2012). Depth specialist coral genera

such as *Leptoseris* have skeletal structures that enable the absorption of more light than shallow water *Porites* (Kahng et al., 2012). In combination with an arrangement of symbiont cells in a mono-layer, corals of the mesophotic genus *Leptoseris* maximize light capture and photosynthetic efficiency under low light conditions (Schlichter et al., 1986). Additionally, the association with different symbionts is a factor interacting with depth stratification of certain coral species (Rowan and Knowlton, 1995). For instance, the ability to associate with different *Symbiodinium* types along light gradients may be a trait of some depth generalist corals broadening their vertical distribution range (Bongaerts et al., 2010). In this regard, some *Symbiodinium* depth specialist types have been designated because they have only been observed in deep water and low light environments so far. These putative specialist types are C79 in *S. pistillata* from the southern Great Barrier Reef (Sampayo et al., 2007), type C11, C11N4, C3N5, CN8 in *Agaricia* on Curacao (Bongaerts et al., 2013), and type C Mcav5 in *Montastraea cavernosa* in the Bahamas (Lesser et al., 2010). In the case of the coral species *Madracis pharensis*, a study showed that coral colonies switched from a generalist symbiont type (B7) to a depth specialist (B15) in deeper water (Frade et al., 2008b). The latter symbiont contained more photosynthetic pigments per cell and had different pigment ratios, possibly explaining the superior photophysiological efficiency in its host compared to symbiont-generalist hosting coral species (Frade et al., 2008a). This does not seem to be a universal mechanism though (Cooper et al., 2011; Bongaerts et al., 2013), as generalist symbiont types, like e.g., type C1, can have large bathymetric distributions and are found in shallow and mesophotic coral communities alike (Chan et al., 2009; Cooper et al., 2011). Despite these potentially important mechanisms in depth acclimatization of corals, the interaction of changing *Symbiodinium* communities and photophysiological capacity are still poorly explored factors as to their role in shaping mesophotic coral communities.

Mesophotic coral ecosystems are receiving increased attention owing to their potential as deep coral refuges in times of global environmental change (see review Lesser et al., 2009; Kahng et al., 2014). Around the Arabian Peninsula, research on mesophotic coral systems has a long tradition, but studies have been geographically limited to the northern Red Sea, i.e., in the Gulf of Aqaba (Fricke and Knauer, 1986; Schlichter et al., 1986; Fricke et al., 1987; Muscatine et al., 1989; Schlichter and Fricke, 1991; Kaiser et al., 1993; Stambler et al., 2008; Alamaru et al., 2009; Einbinder et al., 2009; Mass et al., 2010; Nir et al., 2011). On a global scale, only few studies have investigated the ecophysiology of mesophotic corals under the consideration of the genetic identity of the *Symbiodinium* community (Lesser et al., 2010; Cooper et al., 2011; Nir et al., 2011). Comprehension of coral functioning over large depth gradients in a holobiont framework is critical to our understanding of the role of mesophotics as potential refuges for shallow-water coral communities. Here, we examined mechanisms of coral holobiont photoacclimatization in the mesophotic central Red Sea through collection of ecological, physiological, and molecular data of coral host and *Symbiodinium* from the four coral genera *Porites*, *Leptoseris*, *Pachyseris*, and *Podabacia*.

MATERIALS AND METHODS

CORAL COLLECTION

Corals were sampled in accordance with ethical standards for the care and use of invertebrate animals and KSA Law for Ethics of Research on Living Creatures (National Committee on BioEthics Guidelines as published by King Abdullah Center for Science and Technology). The Saudi Arabian Coastguard Authority issued sailing permits to the sites that include coral collection. Coral fragments were collected using SCUBA and technical diving at the midshore reef Al Fahal (N22°15.100 E038°57.382) in the Saudi Arabian central Red Sea in November 2012. One fragment from the central upward-facing surface per colony of *Porites* spp., *Leptoseris* spp., *Pachyseris speciosa* and *Podabacia* sp. was taken in 10 m intervals between 1 and 60 m (i.e., 1 m, 10 m, 20 m, 30 m, 40 m, 50 m, 60 m). Due to variable vertical distribution, not all corals could be sampled at each depth (see sample distribution in Figure 1).

ENVIRONMENTAL PARAMETERS

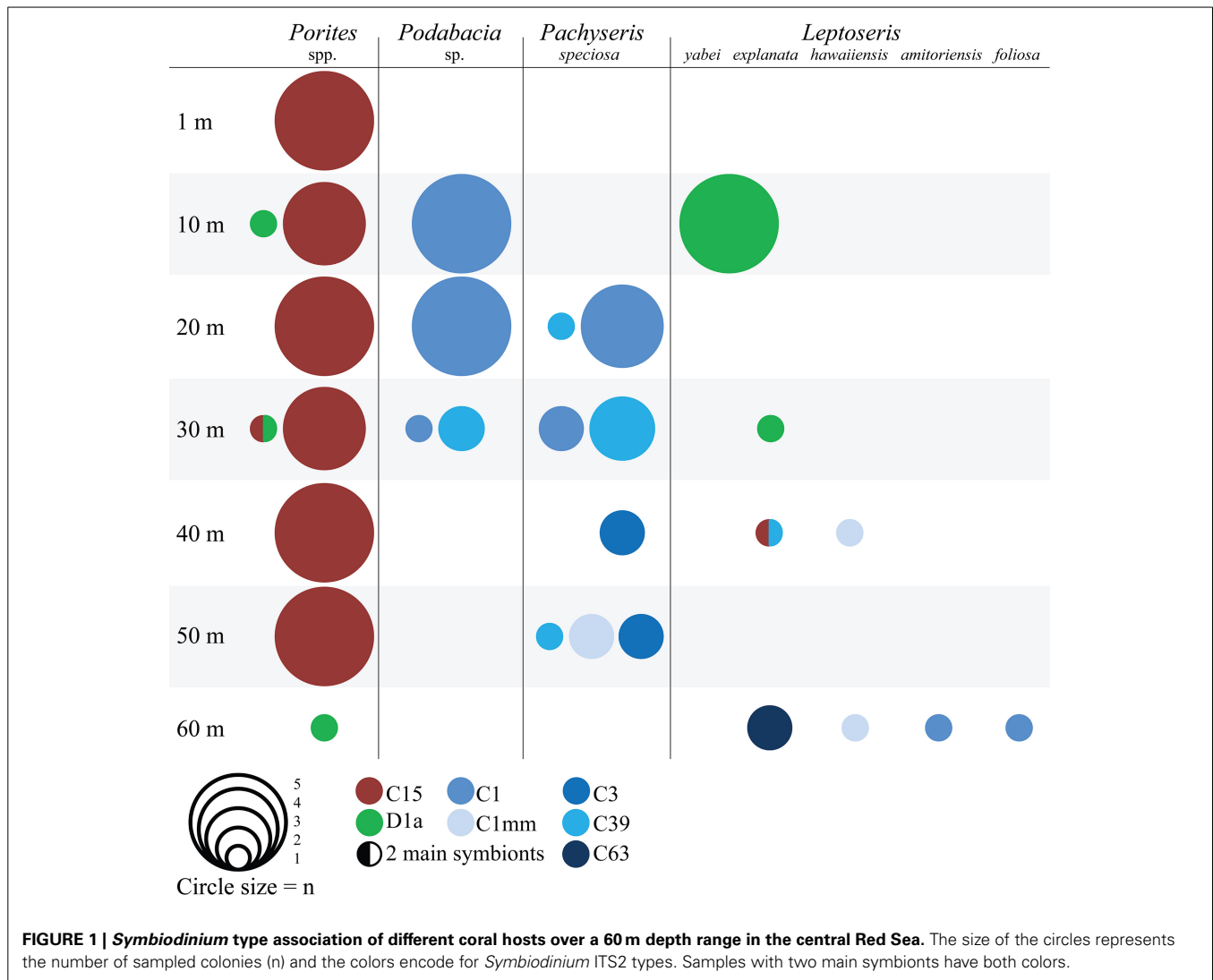
On three days around noon in September 2012, conductivity-temperature-depth (CTD; SBE 16plusV2, Seabird Electronics, USA) and light casts (320–900 nm, Ramses-ACC-VIS, TriOS GmbH, Germany) were performed to 60 m depth in close proximity to the sampling location measuring photosynthetic active radiation (PAR), spectral irradiance, water temperature, salinity, oxygen saturation, chlorophyll fluorescence, and turbidity approximately every 5 m.

CORAL PROCESSING AND MEASUREMENTS

Each collected specimen ($n = 76$) was separated in two pieces: one small piece was rinsed with filtered seawater and snap-frozen in liquid nitrogen for subsequent analyses (see below). The remaining bigger fragment was incubated in the dark for approx. 60 min after which maximum quantum yields (F_v/F_m) were measured three times with a Diving Pulse-Amplitude-Modulated (PAM) Fluorometer (Walz, Germany) using default settings.

Coral tissue was removed from snap-frozen pieces with ice-cold 4% NaCl solution using a standard airgun and an airbrush (Airbrush-starter-set, Conrad Electronic SE, Germany) at 6–8 and 2 bar air pressure respectively. After homogenization of tissue, aliquots were taken for *Symbiodinium* counts, *Symbiodinium* typing, and protein analysis. The remaining slurry was centrifuged for 5 min at 3220 g and the supernatant was removed. The symbiont pellet was washed and resuspended twice before shock-freezing in liquid nitrogen for HPLC analysis of *Symbiodinium* pigments. All processing steps were conducted on ice. Tissue-less coral skeletons were photographed and their surface area determined using CPCe v4.0 (Kohler and Gill, 2006) against a reference scale, which was placed on each picture.

Symbiodinium densities were determined with six replicate counts in a Neubauer-improved haemocytometer on a light microscope and calculated per coral surface area. The shock-frozen symbiont samples were dried and extracted in 90% methanol with 1 mM Tris as detailed in Ziegler et al. (2014). Pigment extracts were separated on a reverse-phase HPLC column (18C Chromolith, Merck, Germany) using a linear gradient system with two solvents after Papagiannakis et al. (2005).



All pigments were measured using a Hitachi L-2455 diode array detector (VWR; Germany) and quantified against pigment standards for chl a and c₂, β-car, ddx and dtx according to Papagiannakis et al. (2005) and for per (DHI, Denmark) according to Ziegler et al. (2014). The ratio of LH pigments (i.e., chl α, chl c₂, per) to PP pigments (i.e., β-car, ddx, dtx), and the xanthophyll de-epoxidation ($\text{dtx} / (\text{dtx} + \text{ddx})^{-1}$) were calculated.

Total protein content of tissue slurry was determined after Lowry et al. (1951) against a bovine serum albumin standard (DC protein assay, Bio Rad, Germany) with a spectrophotometer (SpectraMax Paradigm, Molecular Devices, USA). Prior to measurement the samples were extracted in 0.5 M NaOH for 30 min at 90°C.

SYMBIODINIUM COMMUNITY COMPOSITION

Symbiodinium community composition was analyzed via Denaturing Gradient Gel Electrophoresis (DGGE; Cipher DGGE system, CBS Scientific Company, CA) of the ITS2 region. Briefly, DNA was extracted from the tissue slurry using Chelex 100 resin (100–200 mesh, Sigma, USA) and DNA concentrations were

determined using the Qbit dsDNA HS Assay kit (Invitrogen, USA). PCR amplification of the symbiont ITS2 region was conducted according to Ziegler et al. (2014) using the forward primer “ITS2intfor” and the reverse primer “ITS2CLAMP” that contains a GC clamp (LaJeunesse and Trench, 2000). PCR products were separated by electrophoresis for 16 h at 150 V and 60°C on a 8% polyacrylamide denaturing gradient gel (45–80% urea-formamide gradient) (LaJeunesse, 2002). Further processing, reamplification, and sequencing was conducted as detailed in Ziegler et al. (2014). Briefly, representative bands were selected for sequencing to determine the ITS2 type of each sample. Chromatograms of the ITS2 sequences were checked, edited manually, and aligned with Geneious 4.8.4, and BLASTed against GenBank nr database for ITS2 type designation and verification of DGGE fingerprints.

STATISTICAL ANALYSES

Correlation analyses were conducted over depth for physiological parameters. We partitioned the samples by *Symbiodinium* type association and conducted analyses on three datasets: 1) All

samples, i.e., the whole data set ($n = 76$), (2) Subset C1 consisting of 24 coral samples from *Leptoseris*, *Pachyseris*, and *Podabacia*, and (3) Subset C15 consisting of 29 *Porites* samples. Subsets C1 and C15 were selected based on *Symbiodinium* association of the coral host (harboring *Symbiodinium* of either type C1 or C15).

Additional analyses were conducted in a comparative coral host-*Symbiodinium* framework, using the overlapping distribution of *Podabacia* and *Pachyseris* hosting *Symbiodinium* type C1, and *Porites* hosting *Symbiodinium* type C15 at 20 and 30 m. Before pooling the samples over depth, Student's *T*-tests were performed to investigate physiological differences between the two depths per species, which showed no significant difference in *Porites* and *Pachyseris*. In *Podabacia*, only one sample from 30 m was included in the analysis and the respective values were within the range of the samples from 20 m. An analysis of variance (ANOVA) for significant differences between these three host-symbiont combinations aided the detection of host and symbiont effects. Tukeys' *post-hoc* comparison was used when appropriate. For some analyses, the assumptions of homogeneity of variance could not be met and a non-parametric Kruskal-Wallis test on ranks was conducted.

To identify combinations of abiotic water parameters that "best explain" the multivariate physiological pattern of the coral samples, a biota-environmental matching (BIOENV) routine was computed with 99 permutations based on Euclidean distances using PRIMER v6 software (Clarke and Gorley, 2006). This analysis maximizes Spearman rank correlations between the resemblance matrices through permutation of all trial variables. Input data were normalized prior to analysis by subtracting the variable's mean from each value and dividing it by the standard deviation using PRIMER normalization option.

RESULTS

DEPTH STRATIFICATION OF ENVIRONMENTAL PARAMETERS

Light intensity decreased exponentially with depth. While $1200 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ reached to just below the surface at noon, only 1% of this light reached 60 m depth. Hyperspectral scans revealed a strong wavelength specific extinction with water depth (**Figure 2A**). Water temperature decreased from 30.5°C at the surface to 25.5°C at 60 m. Oxygen saturation decreased from 93% to 77% and chlorophyll increased from 0.08 mg m^{-3} to 1.0 mg m^{-3} from the surface to 60 m (**Figure 2B**). Turbidity (NTU 0.12 ± 0.02 SD) and salinity (PSU 39.42 ± 0.14 SD) remained stable over the depth gradient (not shown). Analyses applying the BIOENV routine identified light intensity as the variable best explaining the multivariate pattern of the physiological dataset (described below) on its own ($r = 0.177$, $p = 0.03$). Next best were combinations of a second explanatory variable with light intensity (light + temperature $r = 0.149$; light + chlorophyll $r = 0.133$). As explanatory variables, salinity, turbidity, and oxygen saturation were of minor importance.

CORAL-SYMBIODINIUM ASSOCIATION OVER DEPTH

Analysis of *Symbiodinium* associated with coral samples revealed five distinct ITS2 sequences of known types (C1, C3, C15, C39, D1a), and 2 novel sequences (type C1mm: GenBank Accession Number [ACN] KJ493788, type C63: ACN KJ493789). Both novel ITS2 sequences had high sequence similarity to *Symbiodinium goreau* (type C1: ACN AF333515, Lajeunesse, 2001). Additionally, DGGE profiles of these samples faintly contained the original *S. goreau* C1 band and vice versa (**Figure 3**), and it is likely that C1 represents an intra-genomic variant of the ITS2 rDNA of these novel symbiont types (Thornhill et al., 2007),

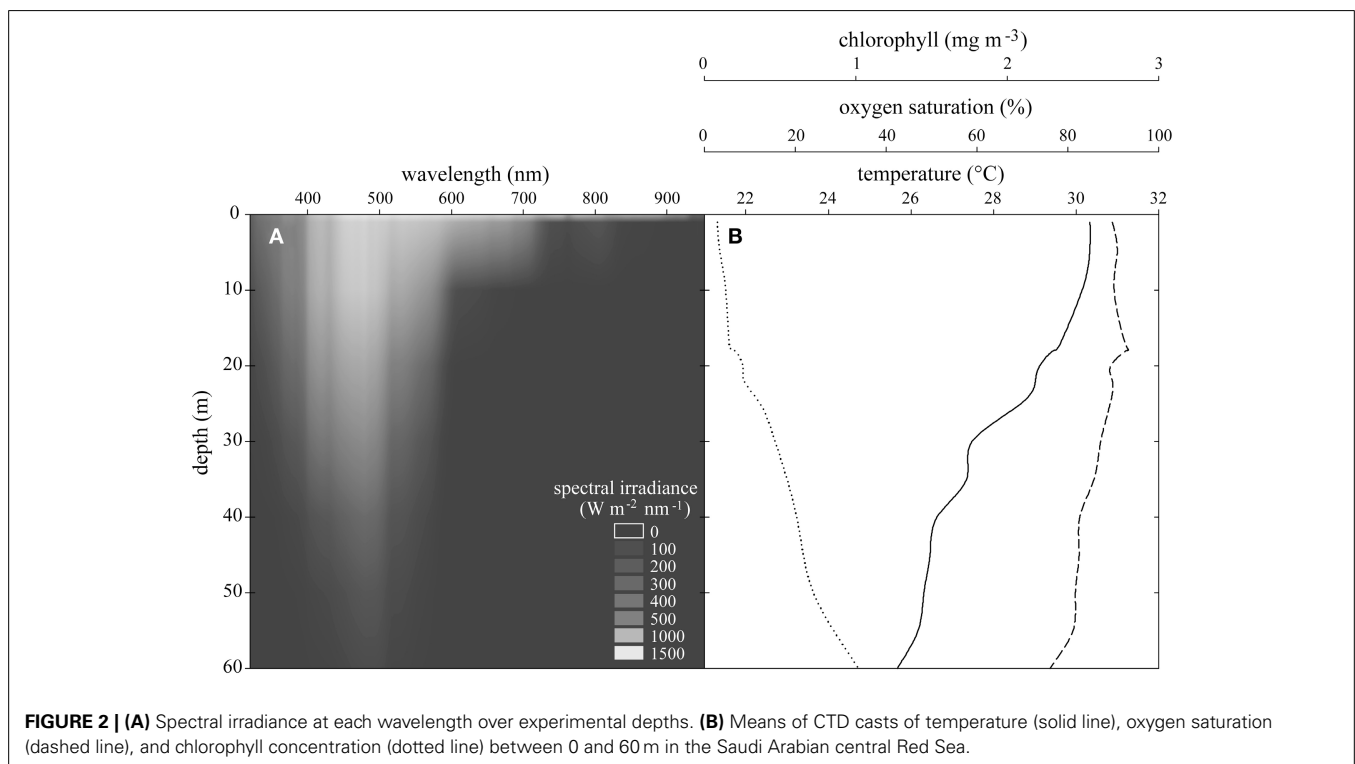
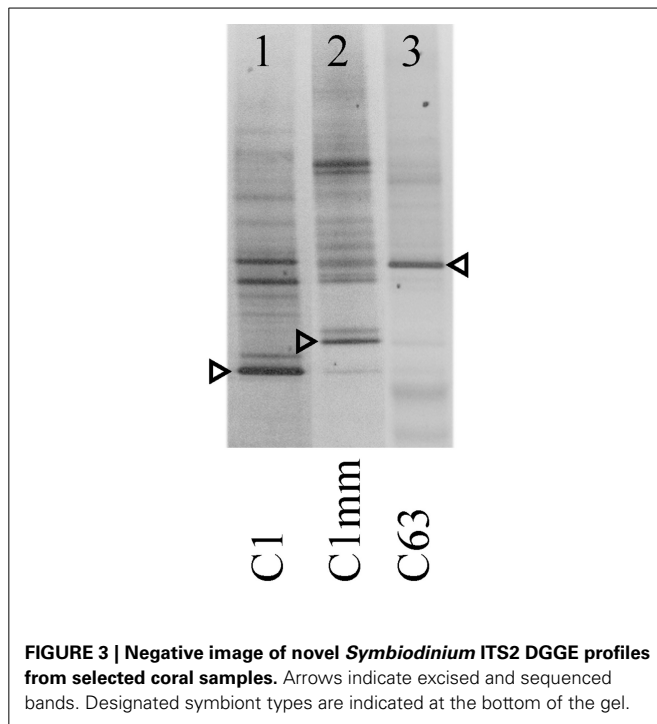


FIGURE 2 | (A) Spectral irradiance at each wavelength over experimental depths. **(B)** Means of CTD casts of temperature (solid line), oxygen saturation (dashed line), and chlorophyll concentration (dotted line) between 0 and 60 m in the Saudi Arabian central Red Sea.



suggesting the conversion from a genome dominated by the ITS2 C1 sequence to ones with derived sequences (LaJeunesse, 2005; LaJeunesse and Thornhill, 2011; Thornhill et al., 2014). Yet the novel types, C1mm and C63, exhibited distinct DGGE profiles (Figure 3).

Host-symbiont relationships followed a coral specific pattern (Figure 1): most *Porites* samples harbored *Symbiodinium* type C15 and three colonies harbored type D1a. In *Pachyseris* and *Podabacia* the most common *Symbiodinium* were the widely distributed type C1 and C39, which is identical to C1 with the exception of a 14-base pair deletion. Furthermore, at 40 and 50 m *Pachyseris* associated with *Symbiodinium* types C3 and C1mm. The different species of *Leptoseris* associated with *Symbiodinium* types D1a (*L. yabei*, *L. explanata*), C1 (*L. amatoriensis*, *L. foliosa*), C1mm (*L. hawaiiensis*), and C15, C39, C63 (all *L. explanata*).

SYMBIODINIUM TYPE DIFFERENCES, DEPTH ACCLIMATIZATION, AND HOST EFFECT

We collected a range of physiological parameters for four coral genera over depth profiles from 1 to 60 m in order to comprehend how depth relates to differences in physiology (Figure 4). To identify which physiological parameters varied over depths, we tested for correlations of physiological parameters to depth considering either all samples ($n = 76$), subset C1 ($n = 24$ from *Leptoseris*, *Pachyseris*, and *Podabacia*), or subset C15 ($n = 29$ from *Porites*) (Table 1). Taking samples from all coral species into account, symbiont cell densities, total protein content, and PP/LH ratios all significantly decreased over water depth, whereas F_v/F_m , cellular chl a content, and β -carotene chl a⁻¹ increased. Other pigment to chl a ratios and the xanthophyll de-epoxidation were not significantly correlated with depth (Table 1). Considering only coral samples with either *Symbiodinium* C1 or *Symbiodinium*

C15 revealed that some traits differed between *Symbiodinium* types. For instance, *Symbiodinium* C15 had higher xanthophyll de-epoxidation rates than C1 and overall, maximum quantum yields were lower in C15 than in all other symbionts (Figure 4). Further, depth-dependent differences between these *Symbiodinium* types were apparent for some parameters: in corals harboring *Symbiodinium* type C15 there was a significant negative correlation between ddx chl a⁻¹ ratio and depth, and F_v/F_m significantly increased with depth, while analyses for corals hosting *Symbiodinium* C1 revealed weak and insignificant correlations for these parameters (Table 1). In contrast, in corals associated with *Symbiodinium* type C1 xanthophyll de-epoxidation and depth were positively correlated, while they were independent in corals hosting type C15 (Table 1).

Next we wanted to understand how physiology differs between coral species that host the same main *Symbiodinium* type. *Podabacia* and *Pachyseris* had overlapping distributions at 20 and 30 m and both hosted *Symbiodinium* type C1 (Figure 1). A comparison between C1-hosting *Podabacia* and *Pachyseris* and C15-hosting *Porites* at 20 and 30 m indicated a significant coral host effect (Figure 5, Supplementary Table 1). *Podabacia* contained significantly more protein than any other coral genus, and at 20 and 30 m symbiont cell densities in *Podabacia* were also higher than in *Pachyseris* and *Porites* (Figure 5). Further, coral host association had a significant effect on photosynthetic pigments. The cellular chl a concentration and the β -carotene chl a⁻¹ ratio were significantly reduced in *Symbiodinium* type C1 in *Podabacia* in comparison to *Pachyseris* and *Porites*. Conversely, *Symbiodinium* type C1 in *Podabacia* contained significantly more peridinin chl a⁻¹ and diadinoxanthin chl a⁻¹ than *Symbiodinium* type C1 in *Pachyseris* and C15 *Porites* (Figure 5). Consequently, the PP/LH ratio was increased in *Podabacia* compared to *Pachyseris* and *Porites*, but this difference was not significant in the non-parametric test on ranks (Supplementary Table 1).

DISCUSSION

COMMON CHARACTERISTICS IN CORAL DEPTH ACCLIMATIZATION

Light availability was exponentially decreasing over the 60 m depth gradient, and it was the best abiotic explanatory variable for changes in holobiont physiology. In comparison, temperature, fluorescence, and oxygen saturation were of minor importance, although their influence on physiological processes cannot be ruled out. Some general trends of light acclimatization could be observed for all central Red Sea corals, and these trends were similar to those reported from studies conducted in other oceans. For instance, the decrease in symbiont cell densities and increase in chl a was comparable to that of other corals over similar depth gradients (Frade et al., 2008a; Cooper et al., 2011), and data from the deep mesophotic Red Sea suggest that the trend continues until corals become azooxanthellate (Fricke et al., 1987; Kaiser et al., 1993).

The ratios of the other pigments to chl a can be modulated to enhance photosynthetic efficiency when light becomes limited (Iglesias-Prieto and Trench, 1994, 1997). We found decreasing PP/LH ratios with depth and this indicates photoacclimatization to low light (Falkowski and Dubinsky, 1981; Dubinsky and Stambler, 2009). Furthermore, the positive correlation of β -car

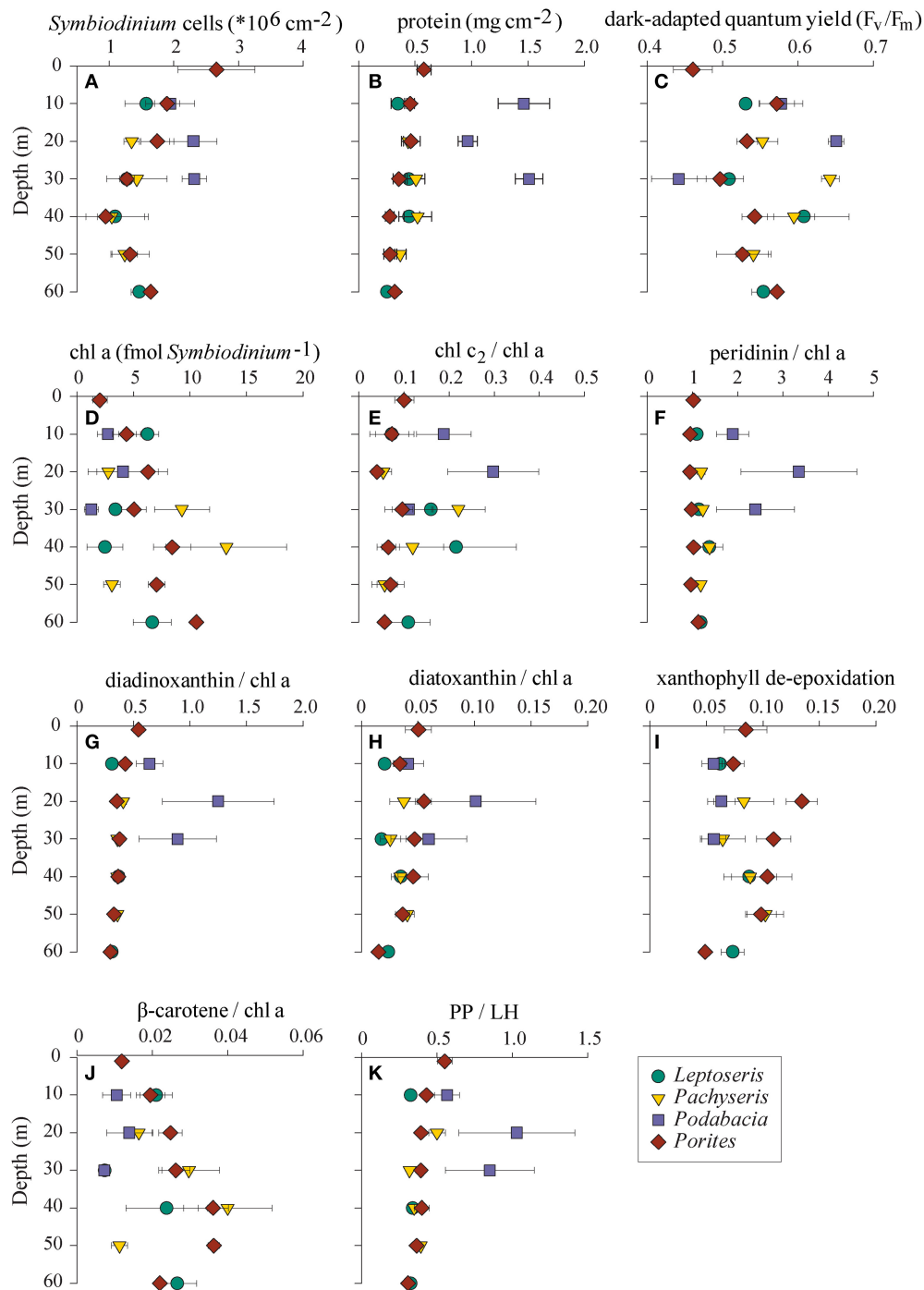


FIGURE 4 | (A–K) Physiological parameters of four coral genera collected in the central Saudi Arabian Red Sea along a 60 m depth gradient (means ± SE) in November 2012. Symbol shapes and colors represent coral hosts:

green circles, *Leptoseria*; yellow triangles, *Pachyseris*; purple squares, *Podabacia*; red diamonds, *Porites*; PP/LH, photoprotective/light-harvesting pigments.

to chl a with depth suggests that increasing photosynthetic efficiency in deeper water was facilitated by an increased number of PSUs (MacIntyre et al., 2002). However, in contrast to previous studies over mesophotic gradients, here ratios of chl c₂ and per to chl a were not correlated with depth, indicating stable PSU sizes (Kaiser et al., 1993; Lesser et al., 2010; Nir et al., 2011), although

we cannot exclude that intra-colony differences at other sites of a given colony exist.

CORAL-SYMBIODINIUM DEPTH STRUCTURE AND PARTITIONING

Coral-*Symbiodinium* association on the upward-facing surface of the colonies followed a host-specific rather than a depth-specific

pattern supporting data from the Great Barrier Reef (Bongaerts et al., 2011) and the Caribbean (Bongaerts et al., 2013). Although one species of *Leptoseris* hosted clade D symbionts in shallow water and other corals of this genus were associated with clade C symbionts in deep water, there was no symbiont species overlap between depths, and hence we could not identify depth-dependent shifts of the main *Symbiodinium* types as reported for other coral species (Frade et al., 2008b; Lesser et al., 2010; Cooper et al., 2011).

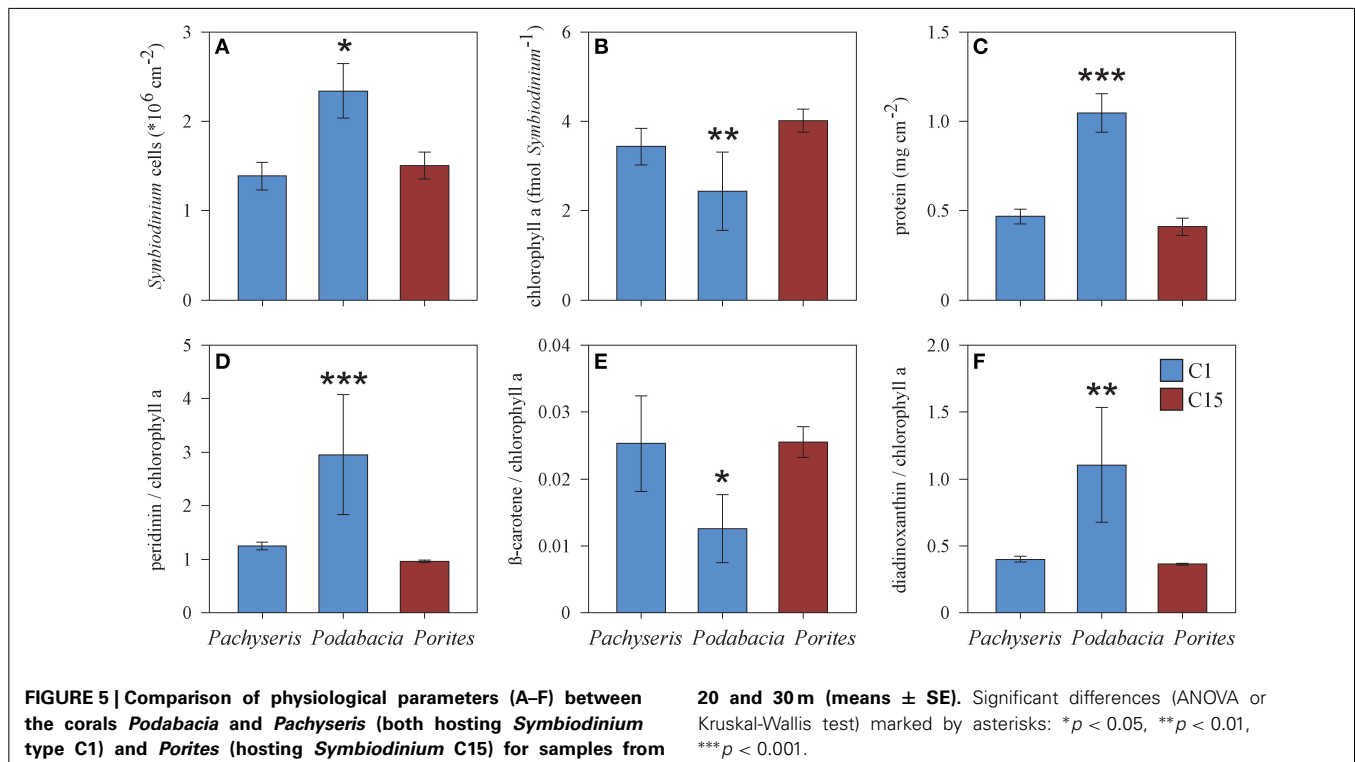
Table 1 | Correlation between physiological parameters and depth for three sets of samples: all samples ($n = 76$), subset C1 ($n = 24$), subset C15 ($n = 29$).

Coral holobiont physiology	Correlation (r) with depth in sample subsets		
	all samples	C1	C15
<i>Symbiodinium</i> cells (10^6 cm^{-2})	-0.49	-0.45	-0.69
Protein (mg cm^{-2})	-0.40	-0.73	-0.68
PP LH^{-1}	-0.23	-0.35	-0.60
F_v/F_m	0.10	-0.26	0.24
chl a ($\text{fmol Symbiodinium}^{-1}$)	0.34	0.42	0.63
β -carotene chl a^{-1}	0.36	0.55	0.79
Diadinoxanthin chl a^{-1}	-0.22	-0.35	-0.74
Diatoxanthin chl a^{-1}	-0.14	-0.21	-0.26
chl c_2 chl a^{-1}	-0.10	-0.29	-0.13
Peridinin chl a^{-1}	-0.10	-0.31	0.13
Xanthophyll de-epoxidation	0.06	0.43	0.02

Significant correlations ($p < 0.05$) in bold.

Symbiodinium type C15 is the most common type in the genus *Porites* in the Red Sea and Western Indian Ocean (LaJeunesse, 2005; Barshis et al., 2010), and our study extends the co-distribution of *Porites* with C15 into the mesophotics (LaJeunesse, 2005). Further, these findings underline the relative specificity of *Porites* species with clade C in the Indo-Pacific (LaJeunesse et al., 2008; Silverstein et al., 2012). In the Persian Gulf, *Porites* is associated with C3 (Hume et al., 2013). C3 represents another generalist symbiont type in Indo-Pacific reefs (LaJeunesse et al., 2003, 2004), which we encountered twice in deep-dwelling colonies of *Pachyseris*, but not in *Porites*. *Symbiodinium* C39 from *Pachyseris* and *Podabacia* in this study has previously been identified as a locally prevalent symbiont in Mussidae and *Diploastrea* in the Red Sea (LaJeunesse, 2005).

Our data suggest that photosynthetic properties of *Symbiodinium* play a role in the vertical distribution range of their coral host. For instance, the higher PP xanthophyll de-epoxidation in *Symbiodinium* type C15 may facilitate the occurrence of *Porites* even in very shallow water where they are exposed to light intensities that can potentially impair the photosynthetic apparatus (Brown et al., 1999). This advantage may offset the overall lower maximum photosynthetic yield of *Symbiodinium* type C15. *Porites* has a broad bathymetric distribution and this is reflected by *Symbiodinium* type C15 that showed a strong photoacclimatory signal. For instance, a negative correlation of ddx to chl a with depth indicates that PP pathways are downregulated when light is scarce (Frank and Cogdell, 1996; Brown et al., 1999). At the same time, the LH potential in deeper water was increased by harboring more cellular chl a along with increasing β -carotene to chl a ratios (MacIntyre et al., 2002). Although *Symbiodinium* type C1 has been found to be



associated with their coral host over large (mesophotic) depths ranges in other locations (Chan et al., 2009; Cooper et al., 2011), all corals associated with *Symbiodinium* type C1 in this study demonstrated limited vertical distributions and only weak or no photoacclimatory signals.

We did not observe a depth-specialist *Symbiodinium* type, but the details of the observed host-*Symbiodinium* associations suggest an influence of the host species on the physiology of its symbiont. Our data show that the coral host had a significant effect on the photosynthetic pigments of *Symbiodinium*. For instance, *Symbiodinium* type C1 in *Podabacia* had two- to three-fold higher per to chl a ratios and two-fold higher ddx to chl a ratios. In contrast, β -carotene to chl a ratios were decreased and *Symbiodinium* type C1 in *Podabacia* contained significantly less chl a than *Symbiodinium* type C1 in *Pachyseris*. *Podabacia* also contained higher densities of *Symbiodinium* cells and protein in its tissues per coral surface area, indicating high tissue biomass (Stimson et al., 2002). Taken together this suggests *Symbiodinium* type C1 in *Podabacia* occur in higher densities and consequently store less accessory chl a, while light capture is optimized through larger LH antennae (Hofmann et al., 1996; Iglesias-Prieto and Trench, 1997). On the other hand, the physiology of the distinct *Symbiodinium* -types in the two host species *Porites* and *Pachyseris* was highly similar to each other, indicating the same “physiological strategy” was employed despite different host and symbiont environments. The direct influence of different coral species on photosystem structure in the same *Symbiodinium* type expands previous findings by Krämer et al. (2013) who found varying PP pigment capacity in the same *Symbiodinium* type hosted by different coral species. As in our study, tissue biomass was different between coral species and Krämer et al. (2013) conclude that these differences exert an influence on the internal light regime for *Symbiodinium*, because host tissue thickness determines light absorption (Dimond et al., 2012). Another notion that may explain the observed coral host effect could lie in the hyperdiversity of LH protein-encoding genes that have been revealed in genomic surveys of *Symbiodinium* (Reichman et al., 2003; Boldt et al., 2012). Differential expression of these and other photosynthesis genes is generally possible (Baumgarten et al., 2013), but its interaction with coral host factors has not been tested. Finally, it cannot be ruled out that host specific physiological differences in *Symbiodinium* C1 may be attributed to fine-scale genetic divergence not resolved by the ITS2 marker, which has previously been demonstrated for *Symbiodinium* B1 (Santos et al., 2004), C3 (Thornhill et al., 2014), and to a much lesser extent for C1 (Thornhill et al., 2014).

Taken together, our data support a view that acclimatization of corals over depth is at least partially facilitated by *Symbiodinium* physiology. The symbiont physiology (e.g., *Symbiodinium* pigment composition and cell densities) in turn is host-specific as highlighted by comparative analysis of different coral species harboring the same main *Symbiodinium* type. This underlines the importance of studying interactions of coral hosts and *Symbiodinium* types as drivers of acclimatization in order to gain further insight into the ecology of mesophotic coral communities. Increasing our understanding of the biology of mesophotic corals is important to better comprehend their

potential role as coral refuges in regard to global environmental change.

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SUPPLEMENTARY MATERIAL

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