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Niche acclimatization in Red Sea corals is dependent on flexibility of host-symbiont association

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ABSTRACT: Knowledge of host-symbiont specificity and acclimatization capacity of corals is crucial for understanding implications of environmental change. Whilst some corals have been shown to associate with a number of symbionts that may comprise different physiologies, most corals associate with only one dominant *Symbiodinium* species at a time. Coral communities in the Red Sea thrive under large fluctuations of environmental conditions, but the degree and mechanisms of coral acclimatization are largely unexplored. Here we investigated the potential for niche acclimatization in 2 dominant corals from the central Red Sea, *Pocillopora verrucosa* and *Porites lutea*, in relation to the fidelity of the underlying coral-symbiont association. Repeated sampling over 2 seasons along a cross-shelf and depth gradient revealed a stable symbiont association in *P. verrucosa* and flexible association in *P. lutea*. A statistical biological-environmental matching routine revealed that the high plasticity of photophysiology and photopigments in the stable *Symbiodinium microadriaticum* (type A1) community in *P. verrucosa* were correlated with environmental influences along spatio-temporal dimensions. In contrast, photophysiology and pigments were less variable within each symbiont type from *P. lutea* indicating that niche acclimatization was rather regulated by a flexible association with a variable *Symbiodinium* community. Based on these data, we advocate an extended concept of phenotypic plasticity of the coral holobiont, in which the scleractinian host either associates with a specific *Symbiodinium* type with a broad physiological tolerance, or the host-symbiont pairing is more flexible to accommodate for different symbiont associations, each adapted to specific environmental settings.

KEY WORDS: Phenotypic plasticity · *Symbiodinium* · Symbiosis · Acclimatization · Coral reef · Red Sea · *Pocillopora verrucosa* · *Porites lutea*

INTRODUCTION

Hermatypic corals live in obligate symbioses with photosynthetic dinoflagellate endosymbionts from the genus *Symbiodinium*. Together, the coral host and algal symbionts are adapted to live under warm and oligotrophic conditions of tropical and subtropical oceans and constitute the foundation of coral reefs, which are among the most productive and diverse marine ecosystems (Connell 1978).

Corals differ in their ability to adjust to varying environmental settings. For instance, some corals are able to acclimatize to a large range of light conditions, which results in a broad light and/or depth distribution. Flexible coral species can alter coral colony growth form (Einbinder et al. 2009) or production of

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photoprotective compounds (Dunlap & Shick 1998, Salih et al. 2000) to influence the internal light regime. In *Symbiodinium*, the ratio and composition of light-harvesting pigments, such as chl *a*, chlorophyll c_2 (chl c_2), and peridinin (peri), can be modulated to optimize size and number of photosynthetic units per symbiont cell (Iglesias-Prieto & Trench 1994, 1997, Hennige et al. 2009). The adjustment of photopigments is often accompanied by a change in *Symbiodinium* cell densities (Frade et al. 2008). Further, the photoprotective pigments diadinoxanthin (Ddx) and diatoxanthin (Dtx) dissipate excess light energy through the de-epoxidation of Ddx to Dtx (Brown et al. 1999) and together with β-carotene (β-car) they aid in the stabilization of the photosystem (PS) structure under light stress (Frank & Cogdell 1996). Consequently, with increasing light, *Symbiodinium* harbor more photoprotective pigments in relation to light-harvesting pigments (Hennige et al. 2009).

Light acclimatization mechanisms increase photosynthetic efficiency (Lesser et al. 2010), which can be assessed for photosystem II (PSII) using pulse-amplitude-modulated (PAM) fluorometry *in situ* (Ralph et al. 1999). *Symbiodinium* acclimatized to low light intensities feature low maximum electron transport rates (ETR_{max}) and minimum saturating irradiances (E_k), while light use efficiency (α) and effective quantum yields ($\Delta F/F_m'$) are increased (Ralph & Gademann 2005, Frade et al. 2008, Lesser et al. 2010). As natural light levels increase, *Symbiodinium* have increased ETR_{max} and E_k, while α and $\Delta F/F_m'$ follow an opposite trend (Ralph & Gademann 2005).

Genetically distinct *Symbiodinium* types or species differ in their photophysiological properties and acclimatization capacity (Chang et al. 1983, Iglesias-Prieto & Trench 1997, Hennige et al. 2009). Consequently, acclimatization mechanisms of so-called generalist coral species include changes of the *Symbiodinium* community composition along environmental gradients (Baker 2003). For example, it has been shown that some corals associate with different *Symbiodinium* types along depth gradients (Rowan & Knowlton 1995), which may confer a functional advantage to the coral host (Cooper et al. 2011). Furthermore, host-*Symbiodinium* associations may vary in response to a range of environmental factors at different spatio-temporal scales. In several coral species in the Great Barrier Reef, the prevalence of *Symbiodinium* from clade C at offshore locations converge to the prevalence of *Symbiodinium* from clade D with increasing coastal influence (Ulstrup & van Oppen 2003). Comparable changes of *Symbiodinium* communities in response to season are less common (Chen et al. 2005); studies that monitored several coral species over 5 yr demonstrated that most host-*Symbiodinium* combinations are stable over time (Thornhill et al. 2006), although background shuffling (McGinley et al. 2012), and shifting dominance between co-occurring types within the same *Symbiodinium* community does occur (Ulstrup et al. 2008). Taken together, flexible association with *Symbiodinium* types along environmental gradients is an important factor that broadens a coral's distribution range (Rodriguez-Lanetty et al. 2001, Bongaerts et al. 2010). Conversely, inflexible host-*Symbiodinium* associations, for example, as seen in *Pavona gigantea* and *Pocillopora verrucosa* in the Gulf of California, may be limiting a species' depth distribution (Iglesias-Prieto et al. 2004) and render it more vulnerable to environmental change (Buddemeier & Fautin 1993, Berkelmans & van Oppen 2006).

In the central Red Sea, water temperatures undergo large variation and regularly exceed 32°C in the summer (Davis et al. 2011), but little is known about how corals acclimatize to the differences in prevailing environmental conditions. In this study, we assessed whether compensation mechanisms differ between coral species harboring a specific *Symbiodinium* type and corals that are known to associate with a variable *Symbiodinium* community to further understand the interaction between host-*Symbiodinium* specificity and acclimatization potential of the coral holobiont. To address this knowledge gap, we investigated acclimatization mechanisms in 2 dominant central Red Sea corals, *P. verrucosa* and *Porites lutea*, on a spatio-temporal scale that incorporated nearshore vs offshore and seasonal variability. In particular, we were interested in the dynamics of the coral-associated *Symbiodinium* community in relation to photophysiology and pigment composition to identify drivers of seasonal niche acclimatization in this understudied coral reef ecosystem.

MATERIALS AND METHODS

Study location

The study was conducted in the central Saudi Arabian Red Sea along a cross-shelf and depth gradient. Four colonies of *P. verrucosa* and *P. lutea* were sampled at 1, 5, 10, and 20 m each at a nearshore reef, 'Inner Fsar' (22° 13.974' N, 39° 01.784' E), a midshore reef, 'Al Fahal' (22° 15.100' N, 38° 57.386' E), and an offshore reef, 'Shib Nazar' (22° 21.006' N, 38° 51.139' E), located 3, 10, and 25 km from the

shore, respectively. Sampling took place in February and September 2012, during the coldest and hottest months of the year, respectively. As a consequence of a previous bleaching event (Furby et al. 2013), *P. verrucosa* colonies were absent at shallow depths of the nearshore location in February and 2 extra samples from 10 and 20 m were taken. In September we were able to sample re-grown colonies, resulting in a total of 87 samples from *P. verrucosa* and 96 samples from *P. lutea*.

Environmental parameters

Three CTD (SBE 16plusV2, Seabird Electronics) casts were performed per site and season around noon recording data on photosynthetic active radiation (PAR), water temperature, salinity, oxygen saturation, and turbidity. Discrete water samples were taken at the coral sampling depths with 10 l Niskin bottles and analyzed for total suspended matter (TSM), carbon and nitrogen concentrations of TSM and their isotopic ratios reported as ‰ $\delta^{13}C$ and ‰ $\delta^{15}N$ relative to Pee Dee Belemnite standard and atmospheric nitrogen, respectively, as well as chlorophyll content, silicate, and inorganic nutrients (i.e. ammonia, nitrate and nitrite, phosphate) following procedures outlined in Ziegler et al. (2014).

In situ photophysiology

On the sampling days between 09:00 and 10:00 h the light-adapted state of PSII of the coral-associated symbionts was assessed with PAM fluorometry (Ralph et al. 1999). Three effective quantum yields ($\Delta F/F_m'$) and one rapid light curve (RLC) were measured with a Diving PAM (Walz) at 4 positions across the upper, non-shaded part of the colony for *P. verrucosa* (light steps: 106, 176, 271, 435, 560, 769, 1069, 1558 µmol photons m^{-2} s^{-1}) and *P. lutea* (light steps: 90, 175, 244, 348, 437, 620, 819, 1215 µmol photons m^{-2} s^{-1}). The following RLC parameters were calculated using linear regression: minimum saturating irradiance (E_k) and maximum light utilization coefficient (α). Maximum electron transport rate (ETR_{max}) was calculated using the formula: ETR = PAR × ($\Delta F/F_m'$) × 0.5 × A (Genty et al. 1989), where A = absorptance (calculated as A = 1 − reflectance). Reflectance was measured as the fraction of light between 400 to 750 nm reflected by the coral surface following Enriquez et al. (2005) using a Ramses-ACC-VIS spectrophotometer (TriOS).

Sample processing

After *in situ* measurements, a small piece of each colony was collected, rinsed with filtered seawater, and snap-frozen in liquid nitrogen. Coral tissue was removed from the snap-frozen skeletons using an airbrush, slurry and symbiont aliquots were separated by centrifugation and washed according to Ziegler et al. (2014). Paraffin wax dipping was used to measure the surface areas of the bleached skeletons (Veal et al. 2010).

Symbiodinium cell densities were determined with 6 replicate counts in a Neubauer-improved haemocytometer in a light microscope and calculated per coral surface area. Symbiont pigments were extracted from disrupted cells in 90% methanol with 1mM Tris and separated on a Chromolith 18C reverse-phase HPLC column (Merck) and quantified as detailed in Ziegler et al. (2014). The ratio of light-harvesting pigments (chl *a*, chl c_2, peri) to photoprotective pigments (β-car, Ddx, Dtx), and the xanthophyll de-epoxidation (Dtx × [Dtx + Ddx]$^{-1}$) were calculated.

Proteins were extracted by incubation of coral tissue in 0.5 M NaOH for 30 min at 90°C. The protein content was measured according to Lowry et al. (1951) against a bovine serum albumin standard (DC protein assay, Bio-Rad).

Symbiodinium identification via ITS2-DGGE and ITS2 sequencing

DNA extraction and PCR amplification of the *Symbiodinium* ITS2 region were conducted according to Ziegler et al. (2014). Briefly, DNA was extracted using Chelex resin (100–200 mesh, Sigma). For the PCR, the forward primer 'ITS2intfor' and the reverse primer 'ITS2CLAMP' that contains a GC clamp were used (LaJeunesse & Trench 2000). Denaturing gradient gel electrophoresis (DGGE) was conducted to separate the PCR products for 16 h at 150 V and 60°C on an 8% polyacrylamide gel with a 45–80% urea-formamide gradient (LaJeunesse 2002). Denaturing gels were stained with SYBR Safe (Invitrogen), photographed, dominant bands were excised, and subsequent re-amplification and sequencing were conducted as detailed in Ziegler et al. (2014). The ITS2 sequences were edited and aligned with Geneious 4.8.4 and BLASTed against GenBank 'nr' database for ITS2 type designation and verification of DGGE fingerprints.

Statistical analyses

Maximum likelihood Chi-square tests were performed to examine significant differences in the distribution of *Symbiodinium* types across seasons, sites, and depths using the software Statistica 9.1. Permutational multivariate analyses of variance (PERMANOVA) were conducted on overall physiology and for each physiological variable separately to test for significant differences between coral species. Subsequently, we tested for differences in the factors site, season, and the co-variate sampling depth (all fixed) on environmental and coral physiology variables in each species separately. The PERMANOVA routine was run using 9999 permutations with sequential sum of squares and permutation of residuals under a reduced model with post-hoc pairwise comparisons. Multivariate patterns of physiological variables were visualized using non-metric multidimensional scaling (nMDS). Data were log(x + 1) transformed and Euclidean distances computed prior to analyses.

To identify combinations of abiotic water parameters that best explained the multivariate physiological pattern of the coral samples, a biological-environmental matching routine (BioENV) was computed with 99 permutations on Spearman rank correlations between environmental and physiological resemblance matrices. Input data were normalized prior to analysis. All multivariate analyses were run using PRIMER v6 software (Clarke & Gorley 2006).

RESULTS

To understand the relationship between environmental variability and acclimatization mechanisms in a coral host-symbiont framework, we measured 16 environmental (see Fig. S1, Table S1 in the Supplement at www.int-res.com/articles/suppl/m533p149_supp.pdf) and 14 physiological parameters in the corals *Pocillopora verrucosa* (Fig. S2, Table S2) and *Porites lutea* (Fig. S3, Table S3) over 2 sampling times, across 3 sites, and 4 depths.

Coral-*Symbiodinium* associations

Symbiodinium microadriaticum (i.e. type A1) was the prevalent symbiont species in *P. verrucosa* (found in 80 of 87 colonies) across the shelf gradient and over seasons. *Symbiodinium* type A21 (GenBank accession number [ACN]: KF939534), which was recently reported from *P. verrucosa* in the southern Red Sea (Sawall et al. 2014), was found in 4 colonies at the nearshore site (site 3, Fig. 1A). At the offshore site, C15 was observed in a single colony. Two other colonies harbored a novel *Symbiodinium* type designated as C98 (ACN: KJ882303). In contrast, *Symbiodinium* associations of *P. lutea*, were highly plastic and dependent on variable factors such as cross-shelf gradient, depth, and season (Fig. 1A, Fig. 2D). Different *Symbiodinium* types belonging to clade C were prevalent offshore and midshore, while 40% (i.e. 13 of 32 colonies) of nearshore *P. lutea* colonies hosted *Symbiodinium* type D1a (Chi-square test; $p < 0.005$) (Fig. 1). Furthermore, there was a significant depth interaction, with 31 of 32 colonies bearing type C15 symbionts limited to deep (10 and 20 m) water (Chi-square test; $p < 0.001$). In the shallow waters (1 and 5 m), novel C15 variants: C15n (ACN: KJ882299), C15o (ACN: KJ882300), C15p (ACN: KJ882301), and 2 novel types of C97 (ACN: KJ882302) and C99 (ACN: KJ882304), were prevalent instead. Moreover, there was a significant trend from C15n dominance in winter to C15p in summer (Chi-square test; $p < 0.05$).

Environmental patterns

The study sites were subjected to strong seasonal fluctuation, as indicated by more than half of the environmental variables displaying significant differences between winter and summer (Table 1, see Fig. S1 and Table S1 in the Supplement). Water temperature, light intensity, and to a lesser degree, salinity were all significantly higher in summer than in winter (Table 1, Fig. 3A). In contrast, several factors indicating an increase in ecosystem productivity related to nutrient enrichment were increased in winter; these included turbidity, chlorophyll, oxygen saturation, silicate, and phosphate, while $\delta^{13}C$ decreased during winter (Table 1, see Fig. S1, Table S1, and 'Supplemental results' in the Supplement).

Despite the overall oligotrophic conditions in the central Red Sea, we detected a significant gradient of inorganic nutrients, phytoplankton, turbidity, and stable isotopic signature of the suspended matter across sites. In summer, environmental conditions at the offshore site were significantly different from midshore and nearshore sites (pairwise PERMANOVA; $p < 0.005$ and $p < 0.001$, respectively) that were not significantly different from each other ($p > 0.05$). By comparison, in winter the nearshore site was significantly different from midshore and off-

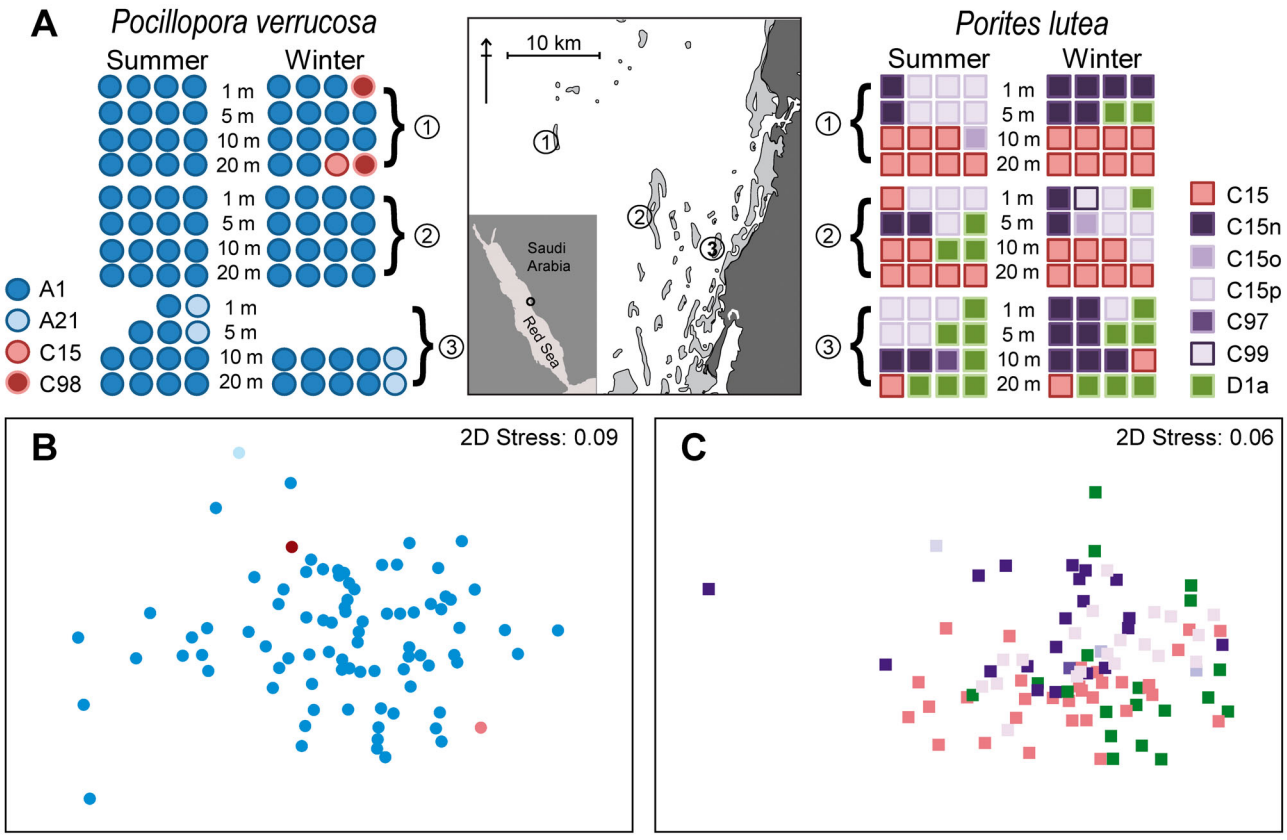

Fig. 1. *Symbiodinium* composition and physiology in colonies of *Pocillopora verrucosa* and *Porites lutea* in the central Red Sea. (A) *Symbiodinium* types across coral samples collected from 3 cross-shelf locations (1 = offshore, 2 = midshore, and 3 = nearshore) and 4 depths (1, 5, 10, and 20 m) in the central Red Sea during summer and winter of 2012. (B,C) Non-metric multidimensional scaling (nMDS) ordination plots of 14 physiological variables measured from samples of (B) *P. verrucosa* and (C) *P. lutea*. Each symbol represents a sample (see panel A for color codes)

shore sites (pairwise PERMANOVA; $p < 0.005$ and $p < 0.001$, respectively), which in turn were not significantly different from each other ($p > 0.05$). Overall, 6 of 16 variables correlated with water depth, resulting in overall significant differences between depths (PERMANOVA; $p < 0.001$) (Fig. 3A, Table 1, see 'Supplemental results' in the Supplement). Based on PERMANOVA pseudo-*F* values for the factors season, site, and depth, 2-dimensional plots were generated as a comparative tool to visualize the weight of the separate variables with respect to these factors (Fig. 3).

Patterns in photophysiology

Seasonal niche acclimatization operated differently in both coral species (Fig. 2A). During winter, ETR_{max} and E_k of *Symbiodinium* cells in *P. verrucosa* were around 1.5 times higher than for those associated with *P. lutea*. In summer, ETR_{max} and E_k significantly increased in *P. verrcuosa* symbionts while they decreased in those of *P. lutea* (Table 2, Figs. S2 & S3, Tables S2 & S3), thereby more than doubling the differences in these variables between both species (Fig. 2B). Other important factors contributing to the seasonal pattern in both species were apparent from chlorophyll fluorescence data, in particular, an increased effective quantum yield of PSII ($\Delta F/F_m'$), and a significant decrease in light use efficiency (α) were observed during winter (Table 2). Furthermore, photophysiology was affected along the cross-shelf gradient in *P. verrucosa* symbionts (Fig. 3C). E_k at the offshore site was significantly increased compared to the nearshore site in winter (pairwise PERMANOVA; $p < 0.005$), and compared to midshore ($p < 0.01$) and nearshore ($p < 0.05$) sites in summer. Light use efficiency α, the only parameter that differed between sites in summer, was stable in winter. During summer, α at the offshore site was significantly lower than at midshore (pairwise PERMANOVA; $p < 0.005$) and nearshore ($p < 0.05$). Photophysiological acclima-

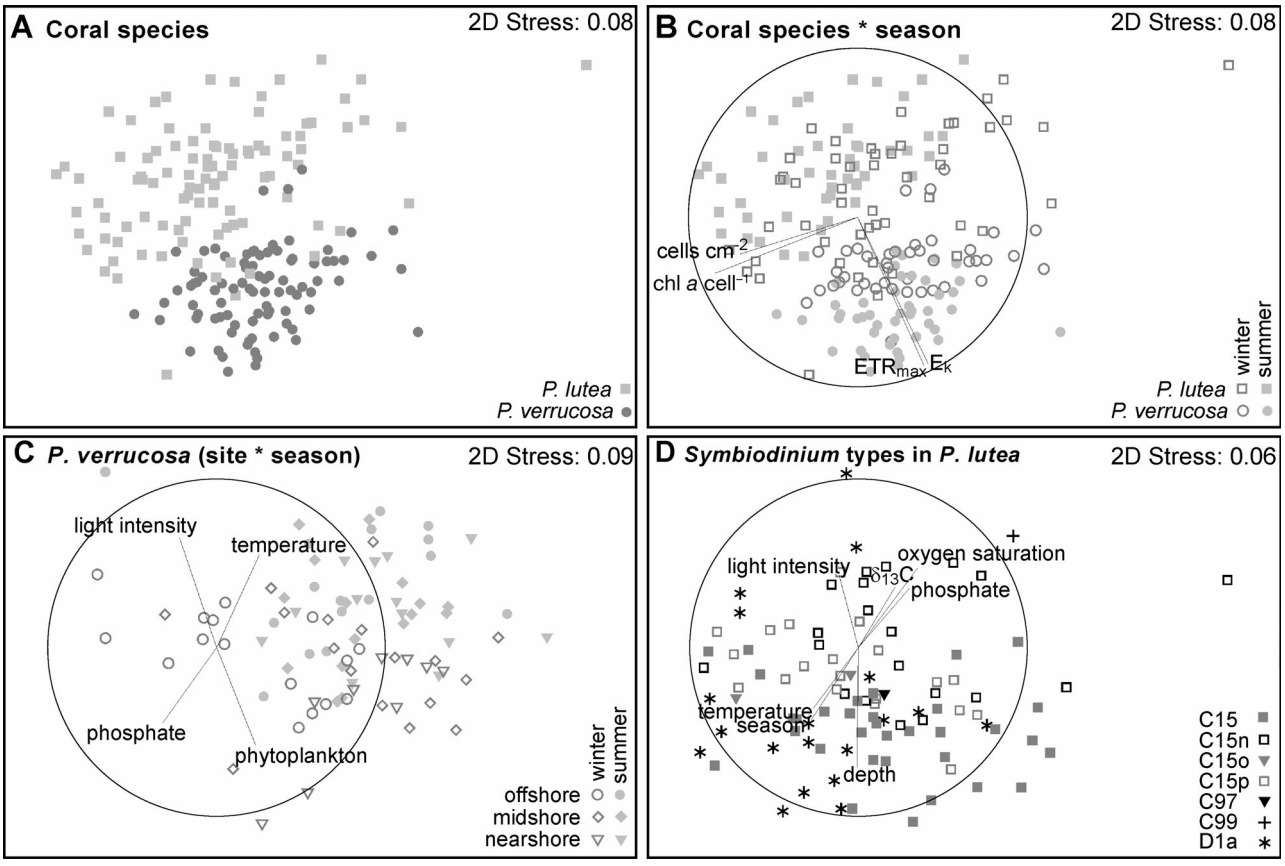

Fig. 2. Non-metric multidimensional scaling (nMDS) ordination plots of physiological parameters in *Porites lutea* and *Pocillopora verrucosa* corals in the central Red Sea; measured in (A) *P. lutea* and *P. verrucosa*, (B) *P. lutea* and *P. verrucosa* during winter and summer seasons, (C) in *P. verrucosa* during winter and summer across 3 cross-shelf locations (nearshore, midshore, offshore) and (D) in relation to *Symbiodinium* types in *P. lutea*. Vector overlays (representing multiple regression correlations) indicate environmental factors contributing most to the separation of data

Table 1. PERMANOVA test results for 16 abiotic variables measured from water samples and CTD casts (n = 72) in the central Red Sea. Analyses are displayed for the factors season (winter and summer), site (nearshore, midshore, offshore), and depth (1, 5, 10, and 20 m). Test results for all variables combined (first row) and variables analyzed separately are shown. TSM = total suspended matter. Significant differences ($p < 0.05$) are shown in **bold**, ns = not significant

Variable	Effect of season		Effect of site(season)		Effect of covariate: depth	
	Pseudo-*F*	p (perm)	Pseudo-*F*	p (perm)	Pseudo-*F*	p (perm)
All variables	17.81	**0.0001**	5.24	**0.0001**	71.93	**0.0001**
Temperature (°C)	1663.3	**0.0001**	3.99	**0.0072**	21.17	**0.0001**
Light intensity (µmol photons m^{-2} s^{-1})	37.48	**0.0001**	4.84	**0.0019**	218.12	**0.0001**
O_2 saturation (%)	178.17	**0.0001**	6.58	**0.0001**	7.93	**0.0052**
Silicate (µmol l^{-1})	64.48	**0.0001**	7.87	**0.0002**	8.28	**0.0046**
Chl *a* (µg l^{-1})	33.44	**0.0001**	7.31	**0.0002**	4.10	**0.0445**
$\delta^{13}C$ of TSM	228.83	**0.0001**	13.17	**0.0001**	1.48	ns
Turbidity (NTU)	29.96	**0.0001**	18.62	**0.0001**	2.35	ns
Salinity (PSU)	9.34	**0.0035**	4.02	**0.0060**	0.59	ns
Phosphate (µmol l^{-1})	144.56	**0.0001**	0.72	ns	0.66	ns
‰ C of TSM	2.43	ns	11.41	**0.0001**	2.76	ns
‰ N of TSM	1.10	ns	9.07	**0.0001**	2.51	ns
C:N of TSM	0.02	ns	3.14	**0.0197**	0.98	ns
Nitrite + nitrate (µmol l^{-1})	0.08	ns	2.42	ns	4.09	**0.0474**
Ammonia (µmol l^{-1})	0.11	ns	0.53	ns	2.67	ns
$\delta^{15}N$ of TSM	0.61	ns	1.73	ns	0.39	ns
TSM (mg l^{-1})	2.01	ns	0.35	ns	0.09	ns

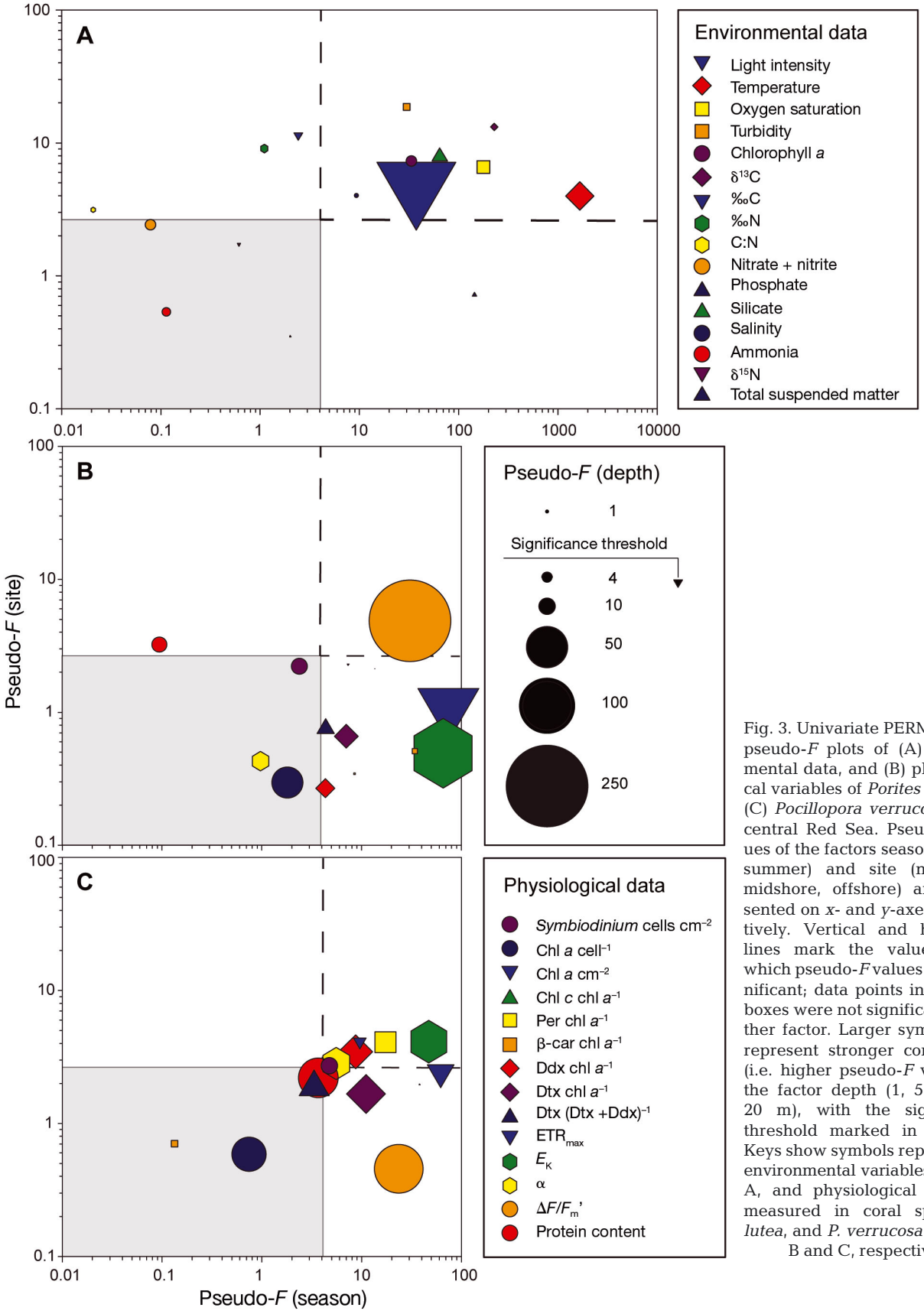

Fig. 3. Univariate PERMANOVA pseudo-*F* plots of (A) environmental data, and (B) physiological variables of *Porites lutea* and (C) *Pocillopora verrucosa* in the central Red Sea. Pseudo-*F* values of the factors season (winter, summer) and site (nearshore, midshore, offshore) are represented on *x*- and *y*-axes, respectively. Vertical and horizontal lines mark the values above which pseudo-*F* values were significant; data points in the grey boxes were not significant for either factor. Larger symbol sizes represent stronger contribution (i.e. higher pseudo-*F* values) of the factor depth (1, 5, 10, and 20 m), with the significance threshold marked in the key. Keys show symbols representing environmental variables in panel A, and physiological variables measured in coral species *P. lutea*, and *P. verrucosa* in panels B and C, respectively

Table 2. PERMANOVA test results for 14 physiological variables in 2 coral species in the central Red Sea. Analyses are displayed for the factors species (*Pocillopora verrucosa* and *Porites lutea*), season (summer and winter), site (nearshore, midshore, offshore), and the covariate factor depth (1, 5, 10, and 20 m). Significant differences ($p < 0.05$) are shown in **bold**, ns = not significant

Variable	Effect of species		*Pocillopora verrucosa*						*Porites lutea*					
			Effect of season		Effect of site (season)		Effect of covariate: depth		Effect of season		Effect of site (season)		Effect of covariate: depth	
	Pseudo-*F*	p (perm)	Pseudo-*F*	p (perm)	Pseudo-*F*	p (perm)	Pseudo-*F*	p (perm)	Pseudo-*F*	p (perm)	Pseudo-*F*	p (perm)	Pseudo-*F*	p (perm)
All variables	86.14	**0.0001**	18.43	**0.0001**	3.54	**0.0005**	19.36	**0.0001**	12.86	**0.0001**	1.97	ns	20.29	**0.0001**
Symbiodinium (cells 10^6 cm^{-2})	8.26	**0.0038**	4.75	**0.0332**	2.71	**0.0365**	10.05	**0.0015**	2.38	ns	2.22	ns	9.52	**0.0024**
Chl *a* (fmol symbiont^{-1})	29.09	**0.0001**	0.74	ns	0.59	ns	43.03	**0.0001**	1.81	ns	0.30	ns	35.64	**0.0001**
Chl *a* (pmol cm^{-2})	1.49	ns	9.60	**0.0033**	4.13	**0.0052**	5.62	**0.0215**	7.34	**0.0093**	2.29	ns	0.12	ns
chl c_2:chl *a*	1.00	ns	37.94	**0.0001**	1.96	ns	0.06	ns	13.61	**0.0001**	2.12	ns	0.00	ns
Peridinin:chl *a*	0.96	ns	17.28	**0.0001**	4.09	**0.0038**	21.46	**0.0001**	8.50	**0.0007**	0.34	ns	0.17	ns
β-carotene:chl *a*	2.85	ns	0.13	ns	0.70	ns	2.20	ns	34.29	**0.0001**	0.51	ns	1.42	ns
Diadinoxanthin:chl *a*	3.00	ns	8.69	**0.0032**	3.46	**0.0096**	30.69	**0.0001**	4.34	**0.0254**	0.27	ns	9.63	**0.0008**
Diatoxanthin:chl *a*	0.15	ns	11.04	**0.0013**	1.67	ns	40.24	**0.0001**	7.04	**0.0049**	0.66	ns	15.27	**0.0001**
Xanthophyll de-epoxidation	4.41	**0.0369**	3.34	ns	1.87	ns	32.01	**0.0001**	4.38	**0.0405**	0.75	ns	10.50	**0.0018**
ETR_{max}	466.32	**0.0001**	61.95	**0.0001**	2.42	ns	25.18	**0.0001**	74.24	**0.0001**	1.11	ns	130.82	**0.0001**
E_k	206.35	**0.0001**	46.98	**0.0001**	4.12	**0.0043**	59.92	**0.0001**	65.77	**0.0001**	0.49	ns	159.57	**0.0001**
α	103.34	**0.0001**	5.56	**0.0213**	2.82	**0.0322**	34.60	**0.0001**	0.97	ns	0.43	ns	12.94	**0.0005**
$\Delta F/F_m'$	47.49	**0.0001**	23.51	**0.0001**	0.46	ns	87.64	**0.0001**	30.61	**0.0001**	4.87	**0.0012**	245.18	**0.0001**
Protein (mg cm^{-2})	2.99	ns	3.67	ns	2.20	ns	57.73	**0.0001**	0.09	ns	3.23	**0.0163**	8.38	**0.0033**

tization operated most strongly along the depth gradient in both species (Fig. 3B,C). ETR_{max} and E_k significantly decreased between 1 and 20 m in symbionts of *P. verrucosa* and *P. lutea*. While the maximum electron transport rate decreased with depth, light use efficiency (α) and effective quantum yield of PSII ($\Delta F/F_m'$) significantly increased in both species (Table 2).

Patterns in photosynthetic pigments

Seasonality of the photosynthetic pigment composition varied between species. In *P. lutea*, Dtx:chl *a*, peri:chl *a* ratios, and xanthophyll de-epoxidation were significantly increased during winter, while chl c_2:chl *a* and β-car:chl *a* ratios were significantly decreased at the same time (Table 2). In *P. verrucosa*, peri:chl *a* and chl c_2:chl *a* ratios behaved similar to *P. lutea,* while Dtx:chl *a*, β-car:chl *a*, and xanthophyll de-epoxidation remained stable (Table 2). Both species displayed increases in symbiont densities and cellular chlorophyll content, leading to significantly increased areal chlorophyll concentrations in summer (24–31%) (Table 2). In addition, in *P. verrucosa* there was also a cross-shelf response during winter with reduced *Symbiodinium* cell densities at the offshore site compared to the midshore site (pairwise PERMANOVA; $p < 0.001$) with no significant difference to the nearshore site ($p > 0.05$). As a consequence, areal chlorophyll concentrations were reduced at the offshore site during winter, compared to the midshore (pairwise PERMANOVA; $p < 0.001$) and nearshore site ($p < 0.05$). Site differences in winter also affected the pigment composition; while peri:chl *a* ratio decreased with distance to shore, Ddx:chl *a* increased (pairwise PERMANOVA; $p < 0.05$). In summer, Ddx:chl *a* ratios at the offshore site decreased to levels similar to those found in the midshore site ($p > 0.05$), whilst the nearshore site was stable between seasons and significantly lower than the midshore site ($p < 0.005$).

General mechanisms of depth acclimatization, as assessed by differences in photosynthetic pigments, operated similarly in both species. For example, proportions of photo-

protective pigments of the xanthophyll cycle decreased with depth in relation to chl *a*. In *P. verrucosa*, Ddx and Dtx decreased 48 and 60%, respectively, from 1 to 20 m depth (Fig. S2, Table S2). In *P. lutea*, Ddx and Dtx decreased by 25 and 57% respectively, from 1 to 20 m depth (Fig. S3, Table S3). Concomitantly, xanthophyll de-epoxidation rates decreased from 1 to 20 m in both species, while β-car, the third photoprotective pigment, was stable across depth. The main light-harvesting pigment chl *a* showed a reversed trend to the photoprotective pigments. Chl *a* in *Symbiodinium* cells increased from 1 to 20 m in both species. Whilst chl *a* almost doubled in *P. verrucosa*, increases in *P. lutea* were smaller. *Symbiodinium* cell densities followed an opposite trend to cellular chl *a* and decreased with depth. Despite reduced *Symbiodinium* densities in deeper water, cellular increases in chl *a* in *P. verrucosa* resulted in significantly increased areal chl *a* concentrations at 20 m compared to 1 m. In *P. lutea*, areal chl *a* did not change with depth and the composition of other light-harvesting components such as chl c_2 and peri were also stable between 1 and 20 m. In *P. verrucosa*, chl c_2:chl *a* ratio was stable, while peri:chl *a* ratio decreased from 1 to 20 m.

Finally, protein content was not significantly different between seasons for both corals (Table 2, Figs. S2 & S3, Tables S2 & S3). Protein content decreased with depth (between 1 and 20 m) by 42% in *P. verrucosa* and by 32% in *P. lutea*.

Link between environmental and physiological patterns in relation to host-symbiont specificity

A biological-environmental matching routine (BIO-ENV in PRIMER) revealed that environmental parameters strongly correlated with a structuring of physiology in *P. verrucosa*. Light intensity and turbidity, together with $\delta^{13}C$ (r = 0.520) or temperature (r = 0.516), best explained the multivariate physiological pattern in *P. verrucosa*. By comparison, for *P. lutea*, the best explanatory variables were light intensity, oxygen saturation (r = 0.214), combined with turbidity (r = 0.212), and light intensity and temperature (r = 0.204), but the structuring was less stringent. The significant correlation of environmental gradients with the physiology of *P. verrucosa* was apparent between sampling times, cross-shelf locations, and depths (Fig. 2C, Table 2). Interestingly, the physiological signature was not significantly different between sites during summer (pairwise PERMANOVA; $p > 0.05$), whilst in winter there were significant differences in physiology at the offshore site compared to the midshore ($p < 0.001$) and nearshore site ($p < 0.01$), which were not significantly different from each other ($p > 0.05$). Overall, physiology in *P. lutea* was less variable and not significantly different along the cross-shelf gradient, whilst significant differences between sampling times and depths were of approximately equal importance (Table 2). Taking these results together with the differences in *Symbiodinium* association, the correlation of environmental gradients with physiology observed in *P. lutea* can be related to distinct physiological properties of the different *Symbiodinium* types over sites, sampling times, and depths (Fig. 1C). In contrast, in *P. verrucosa* the single dominant species *S. microadriaticum* was responsible for the observed large physiological plasticity (Fig. 1B).

DISCUSSION

Our analyses of coral acclimatization mechanisms over time and across sites and depths in a comparative coral host-symbiont framework in the Red Sea revealed that strategic differences between *Pocillopora verrucosa* (with high symbiont specificity) and *Porites lutea* (with high symbiont flexibility) exist, which affect their phenotypic plasticity.

Differences in coral-*Symbiodinium* specificity

The coral host's reproductive mode and symbiont acquisition strategy can have an effect on host-symbiont specificity (LaJeunesse et al. 2004, Stat et al. 2008). Here, both investigated coral species pass on endosymbionts to their offspring (Kojis & Quinn 1981, Kinzie 1993), and despite these similar reproductive strategies, *P. verrucosa* and *P. lutea* had different patterns in the host-symbiont specificity. Most colonies of *P. verrucosa* showed a prevalent association with *S. microadriaticum* as has previously been described for this species in the central Red Sea (Sawall et al. 2014, Ziegler et al. 2014). In contrast, *Symbiodinium* association of *P. lutea* was variable and correlated with spatio-temporal factors such as cross-shelf gradient, depth, and sampling time. The conversion from corals associated with *Symbiodinium* from clade C to those with clade D with decreasing distance to shore corresponds to reports of *Acropora valida* and *Acropora millepora* in the Great Barrier Reef (Ulstrup & van Oppen 2003). In this regard, our findings contribute to the perception of

symbionts from clade D as conferring tolerance towards unfavourable environmental settings on their respective hosts (Berkelmans & van Oppen 2006).

In accordance with our findings, depth stratification of the host-symbiont relationship is common in coral species maintaining variable associations with *Symbiodinium* (Rowan & Knowlton 1995). However, the observed shift between sampling points from dominance of *Symbiodinium* C15n in winter to C15p in summer was unexpected. Whilst seasonality of *Symbiodinium* communities has been observed before in *Acropora palifera* (Chen et al. 2005), most corals exhibit stable *Symbiodinium* associations over time (Thornhill et al. 2006, McGinley et al. 2012). However, this seasonality effect was limited to shallow water, where environmental variability was highest, which has previously been proposed as an explanation for more heterogeneous *Symbiodinium* communities at shallow sites relative to deep sites (Thornhill et al. 2006).

Generally, the flexibility in the association of *P. lutea* with diverse *Symbiodinium* types is remarkable. Despite its high bleaching tolerance, it was assumed that *Porites* had a strict association with *Symbidinium* type C3 in the Persian Gulf (Hume et al. 2013) and with type C15 in the Pacific (Franklin et al. 2012), although *Symbiodinium* from clade G have recently been encountered in background abundances in some colonies of *Porites lobata* in Hawaii (Stat et al. 2013). Contrasting the assumption of *P. lutea* as a symbiont specialist, we found diversity in its association with different novel *Symbiodinium* ITS2 types, suggesting a potential alternative mechanism conferring plasticity along environmental gradients in the Red Sea.

Acclimatization mechanisms and differences between coral species

The photosynthetic properties of *P. verrucosa* identified this species as adapted to high light conditions. For instance, compared to *P. lutea*, $\Delta F/F_m'$, ETR_{max}, and E_k were higher in *P. verrucosa*, and in response to the combined effects of increased light intensities and temperature, and decreased turbidity during summer, ETR_{max} and E_k were both increased in *P. verrucosa*. The same mechanism of increasing E_k and decreasing α was also apparent in *P. verrucosa* with increasing distance to shore, similar to sun-adapted surfaces of *P. damicornis* and *A. valida* that had higher ETR_{max} and E_k compared to shade-adapted surfaces of the same colony (Ulstrup et al. 2008).

Furthermore, *Symbiodinium* cell densities in *P. verrucosa* increased in summer and hence were positively correlated with temperature and light. This increase is contrary to decreasing *Symbiodinium* cell densities in other species during summer (Fagoonee et al. 1999, Fitt et al. 2000) and further corroborates to the notion that *P. verrucosa* constitutes a well acclimatized species to prevailing environmental conditions. In contrast, decreased ETR_{max} and E_k in *P. lutea* during summer conform to photoprotective processes in the symbionts (Jones & Hoegh-Guldberg 2001, Warner et al. 2002), such as non-photochemical quenching, a key mechanism in all photosynthetic eukaryotes, including *Symbiodinium* spp. (Reynolds et al. 2008), to dissipate excess energy as heat through xanthophyll cycling (Li et al. 2009). However, at the same time xanthophyll cycling did not show a clear pattern and thus non-photochemical quenching alone cannot account for the decrease in ETR_{max}. This is consistent with observations across a 60 m depth gradient (Ziegler et al. 2015) and may indicate limited plasticity of photoprotective xanthophyll conversion in this species (Warner & Berry-Lowe 2006), but additional data are needed, e.g. at higher temporal resolution, to draw further conclusions. In addition, near the water surface where light intensities were highest, $\Delta F/F_m'$ of symbionts in *P. lutea* was reduced to levels that are symptomatic of photoinhibition (Brown et al. 1999, Jones & Hoegh-Guldberg 2001). As expected, xanthophyll cycling measured for both coral species increased in shallow water allowing more photoprotection in these brighter environments. On average xanthophyll cycling was higher in *P. verrucosa* than in *P. lutea* symbionts, again demonstrating the stronger acclimatization of the former to the prevailing environmental conditions. Moreover, this species-specific difference in photoprotective activity extends previous findings by Ulstrup et al. (2008) who found higher photoprotective cycling of xanthophylls in symbionts associated with *P. damicornis* compared to those of *A. valida.*

Seasonality of chl *a* content in *Symbiodinium* cells or of areal chl *a*, mediated by changing cell densities, is a common phenomenon in corals (Fagoonee et al. 1999, Fitt et al. 2000). In contrast, reports of seasonal changes of photopigment composition or stoichiometric ratios have been rare, while they are more commonly known from the well-studied depth-mediated light gradients (Kaiser et al. 1993, Lesser et al. 2010). In this study, light harvesting pigment concentrations per symbiont cell more than doubled in *P. verrucosa* and increased 50% in *P. lutea* from 1 to 20 m depth, and seasonal photophysiology of *P. verrucosa* and

P. lutea was also accompanied by changes in photopigment composition. For instance, during summer peri:chl *a* ratios decreased, while chl c_2:chl *a* ratios increased, indicating functional changes in the photosynthetic units as have previously been found in cultures of *S. microadriaticum* (Iglesias-Prieto & Trench 1997) and other *Symbiodinium* types (Hennige et al. 2009). In *P. verrucosa*, enrichment of peri:chl *a* and Ddx:chl *a* ratios further accompanied photophysiological acclimatization along the cross-shelf gradient, suggesting that this process was driven by enrichment of light-harvesting complexes (Hofmann et al. 1996, Niedzwiedzki et al. 2014). Corresponding to the exponential change in light intensity, photophysiological alterations were more pronounced across depths, than between sites, or sampling times. However, despite the apparent connection between depth-mediated light differences and photosynthetic properties, it is important to consider that changes in light intensity do not occur in isolation and that light is only one of several environmental factors interacting with photoacclimatization. For instance, photosynthetic pigment composition was more strongly influenced by seasonal variation than by the depth gradient, signifying a central role of several environmental factors such as temperature, turbidity, and oxygen saturation in shaping the photosynthetic apparatus.

Environmental patterns and physiological plasticity in relation to host-symbiont specificity

The magnitude and pattern of the physiological response to the environmental gradients was different between coral species and dependent on the flexibility of their association with different *Symbiodinium* types. Photophysiological changes in the prevalent species *S. microadriaticum* found in *P. verrucosa* were significant across depths, while they were comparably smaller within each of *P. lutea*'s changing *Symbiodinium* types. In addition to depth-mediated changes in irradiance, several environmental factors were related to ecosystem productivity, and correlated with changes in physiology along the cross-shelf gradient in *P. verrucosa* and its stable community of *S. microadriaticum* (as elucidated by the BioENV analysis). In response to gradients of phytoplankton, turbidity, stable isotopic signature of the suspended matter, and temperature between sites during winter, photophysiological changes in symbionts of *P. verrucosa* followed some typical acclimatization mechanisms, such as increased effective quantum yields and decreased minimum saturating irradiances (Cooper & Ulstrup 2009). In accordance with a decrease of environmental differences, these correlations became less obvious in summer. Conversely, physiology remained stable in *P. lutea* (i.e. only 2 of the 14 variables were different across the shelf for this species compared to 6 variables in *P. verrucosa*), while its *Symbiodinium* community changed along the cross-shelf gradient. Other studies reported comparably small physiological acclimatization for *P. lutea*, e.g. along a gradient of anthropogenic impact in China (Roder et al. 2013) or in an area impacted by large amplitude internal waves in Thailand (Roder et al. 2011). However, *Symbiodinium* identity was not determined in these studies and it remains uncertain as to whether the here-proposed mechanism of symbiont flexibility in *P. lutea* can be generalized. Overall, coral populations along reefs in the Red Sea seem to be connected (Robitzch et al. 2015), but host genotypic divergence may have played a role in the observed host-symbiont pattern in *P. lutea* as has been shown for *Seriatopora hystrix* in the Great Barrier Reef (Bongaerts et al. 2010).

CONCLUSION

In this study, we observed diverging acclimatization mechanisms over time, cross-shelf locations, and depths in *P. verrucosa* and *P. lutea*. While *P. verrucosa* was predominantly associated with *S. microadriaticum* and showed strong physiological response to changing environmental conditions, a highly plastic *Symbiodinium* community in *P. lutea* was associated with distinct physiologies and only minor physiological acclimatization. Based on these data, we advocate an extended concept of phenotypic plasticity towards environmental variability as a consequence of the flexibility in the host-*Symbiodinium* association. Symbiont specialist host corals can associate with a specific *Symbiodinium* type with a high physiological tolerance, allowing for high acclimatization potential of the coral holobiont to a range of environmental conditions, and hence compensating the inflexibility in the host-*Symbiodinium* relationship. This is in contrast to coral species with highly variable *Symbiodinium* communities, where differential association of symbionts adapted to specific environmental settings provides an alternative mechanism of acclimatization. Moreover, our findings challenge previous assumptions of presumed host-symbiont specificity in *P. lutea*, and emphasize the notion that specificity might largely depend on the investigated time scale, environmental space, and sampling effort.

To date, the interactions between environment, coral host, *Symbiodinium* community, and photosynthetic properties are not fully understood. In light of environmental change, it is essential to gain further insights into the complex interplay of these parameters.

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