Extensive phenotypic plasticity of a Red Sea coral over a strong latitudinal temperature gradient suggests limited acclimatization potential to warming

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Global warming was reported to cause growth reductions in tropical shallow water corals in both, cooler and warmer, regions of the coral species range. This suggests regional adaptation with less heat-tolerant populations in cooler and more thermo-tolerant populations in warmer regions. Here, we investigated seasonal changes in the in situ metabolic performance of the widely distributed hermatypic coral Pocillopora verrucosa along 12° latitudes featuring a steep temperature gradient between the northern (28.5°N, 21–27°C) and southern (16.5°N, 28–33°C) reaches of the Red Sea. Surprisingly, we found little indication for regional adaptation, but strong indications for high phenotypic plasticity: Calcification rates in two seasons (winter, summer) were found to be highest at 28–29°C throughout all populations independent of their geographic location. Mucus release increased with temperature and nutrient supply, both being highest in the south. Genetic characterization of the coral host revealed low inter-regional variation and differences in the Symbiodinium clade composition only at the most northern and most southern region. This suggests variable acclimatization potential to ocean warming of coral populations across the Red Sea: high acclimatization potential in northern populations, but limited ability to cope with ocean warming in southern populations already existing at the upper thermal margin for corals.

As a consequence of climate change due to increased emissions of greenhouse gases, sea surface temperatures (SST) have risen by ~0.7°C since the 1950s and are expected to increase further by 0.2°C per decade in tropical seas1. Growth of shallow water corals (Porites spp.) in the Indo-Pacific was found to positively correlate with temperature along latitudinal gradients2, most likely due to higher metabolic activity at warmer temperatures. In both, colder and warmer, regions of a species’ range, however, global warming was repeatedly found to reduce coral growth independently of temperature history3–5, a finding suggesting adaptation of the coral holobiont (coral and/or symbionts) to local thermal regimes6. A reduction of coral growth can have far-reaching ecological consequences given that scleractinian corals are the main bioengineers in modern coral reefs providing a structurally complex habitat for numerous species7.

Reasons for reduced coral growth at temperatures above normally experienced temperatures is likely found in a shortage of energy for calcification. This may happen when the coral’s energy supplying symbionts8,9, dinoflagellates of the genus Symbiodinium (zoxanthellae), are damaged and reduced in numbers under temperature stress10 and/or when energy is compromised for stress-preventing processes, such as the expression of heat-shock proteins11. On the other hand, however, it was found that some coral species seem to be able to adapt to environmental changes (including warming) by changing their Symbiodinium composition to more robust types12–14 or by a rather fast genetic adaptation of a given Symbiodinium type15, which is rather promising outlook in the context of global warming. Furthermore, corals thriving in regions with naturally high water temperatures (>31°C) may serve as a ‘genetic reservoir’ of temperature resistant corals possibly able to populate other geographic regions with lower but increasing water temperatures. For this reason, it is of particular importance...
to investigate underlying mechanisms of thermo-tolerant corals, which will help us to better understand and predict the future of coral reefs.

An ideal system to study the coral’s mechanisms to adjust to different prevailing temperature regimes is the Red Sea. The Red Sea is characterized by a strong temperature gradient with particularly high temperatures in the south (≥ 31.5°C during several months in summer12; Fig. 1a). Parallel to the temperature gradient, the depletion of productive Gulf of Aden waters entering the Red Sea drives a strong nutrient gradient, as indicated by high chlorophyll a (chl a) concentrations in the south and low chl a concentrations in the northern and central Red Sea (Fig. 1b). This latitudinal pattern prevails all year except in winter, when deep mixing replenishes surface layer nutrients in the northern Red Sea and Gulf of Aqaba (Fig. 1b). While high nutrient loads can be detrimental to coral reef ecosystems by promoting growth of macroalgae that compete with corals for light and space2, increased nutrient concentrations can be beneficial at the organismal level by enhancing the coral’s nutritional and energetic status resulting in increased coral growth (tissue and skeleton)3,17,18. The combined effect of increasing temperature and nutrients on corals, however, seems to be species specific19 and depended on the quality of nutrients20. Furthermore, corals featuring a high flexibility in nutrients and energy acquisition (autotrophy versus heterotrophy) overcome thermal stress more likely21,22. Despite a wide range of environmental conditions (including extremes) throughout the Red Sea, coral diversity and reef complexity remain high23. The occurrence of certain coral species throughout this highly differentiated gradient suggests regional adaptation. The Red Sea, thus, constitutes a unique natural laboratory to study the effect of different temperature and nutrient regimes in situ, including conditions considered detrimental in other geographic regions under global change scenarios24.

Here, we investigated the physiological performance and genetic composition of the widely distributed coral species Pocillopora verrucosa (Ellis and Solander, 1786) in a rare large scale in situ study spanning 12 degrees of latitude (i.e. 2,000 km coast line) and including steep environmental gradients (i.e. over 6°C annual mean temperature), as well as two seasons (i.e. summer of September 2011 and winter of March 2012). Special emphasis was given to calcification, as the fundamental process of reef growth and hence the formations of complex and diverse coral reef systems. Additionally, photosynthetic rates (as the primary energy source) and mucus release rates (as a major energy loss), as well as the tissue composition (for nutritional status and energy reserves) were assessed, related to environmental conditions and further to calcification. For our study, we hypothesized that coral populations are adapted to prevailing local conditions, which should be reflected in a low latitudinal pattern in coral performance and a differentiation in the genetic composition from north to south.

Methods

Study sites. Six reefs were chosen along the Saudi Arabian Red Sea coast spanning over 12 degrees of latitude and being separated by ~300 km between each reef (Fig. 1a). They covered a large range of environmental conditions, as previously described by Sawall et al.5: Temperature varied between 21°C–27°C (winter – summer) in the north (1-MAQ) and 28°C–33°C in the south (5-DOG, 6-FAR), and water chlorophyll a (chl a) concentrations varied between 0.04–0.26 µg chl a l−1 (summer – winter) in the north (1-MAQ) and 1.45–2.73 µg chl a l−1 (winter – summer) in the south (6-FAR). Light intensities in 5 m depth ranged between 33 and 44 E m−2 d−1 photosynthetic active radiation (PAR) throughout most of the Red Sea in September 2011 and March 2012, but dropped down to ~20 E m−2 d−1 PAR at the most southern site 6-FAR in summer25. All reefs were at least 3 km away from the coast in order to minimize land-based influences (Fig. 1a). One exception is given in the most northern region, the Gulf of Aqaba, where only rather narrow fringing reefs exist along the coast (Fig. 1a). Here, however, the study site 1-MAQ was more than 10 km from the next small village Maqna. All investigations were carried out at the wave-exposed western sites of the reefs at the reef edge or upper reef slope in 5 m depth.

Metabolic rates. In situ incubations were conducted to measure calcification, photosynthesis, respiration and mucus release rates. The experimental design and in situ incubation setup were described previously for a parallel study on P. verrucosa zooxanthellae physiology26, Briefly, prior to incubations for metabolism measurements, 6 coral fragments from 5 m depth were chiseled off from the central part of 6 colonies (1 fragment per colony) at each study site. Each fragment was glued to a plastic screw and fixed in the reef for acclimatization. At two consecutive days, three fragments per day were individually placed in incubation chambers (plus one coral-free control chamber) at the experimental depth from 0800/0900 to 1600/1700 hrs. The incubation setup (constructed at GEOMAR) consisted of 4 cylindrical acrylic chambers (volume: 950 ml) containing a battery-run stirrer, a water inlet and outlet with one-way valves in front and behind the chamber respectively, a fragment holder and an oxygen sensor. Oxygen sensors were connected to a battery-run data logger, as well as an underwater PAR sensor installed next to the chambers. Each water inlet was connected to a programmable battery-run pump via tubing, which pumped the surrounding water through the chambers every 45 min for 3 min to flush the chambers. Each incubation intervals was 43 min long leading to about 9 incubation intervals per day, 8 incubation intervals were conducted during light conditions, 1 incubation interval during dark conditions in the morning (chambers were covered for that).

During incubations oxygen concentration and PAR were logged every minute. Photosynthesis rates derived from oxygen production rates were related to the corresponding PAR intensities (P-I curves). 3–4 times a day samples for total alkalinity

Figure 1 | Map with study sites and environmental conditions. (a) sea surface temperature and (b) water chlorophyll a concentrations as a proxy for nutrient supply were derived from NASA, Giovanni online data system, developed and maintained by the NASA GES DISC, Ocean Color Radiometry, monthly averaged MODIS-Aqua 4 km. Images represent averaged data from July to September (temperature) or to October 2011(chlorophyll a, late summer) and from January to March 2012 (late winter). Study sites are indicated in a) with 1-MAQ = Maqna, 2-WAJ = Al-Wajh, 3-YAN = Yanbu, 4-JED = Jeddah, 5-DOG = Doga and 6-FAR = Farasan Islands, and the distance from the coast is indicated in brackets.
(TA) measurements were extracted to calculate calcification rates. For this, 100 ml of water was sampled manually with a syringe at the chamber water outlet in the beginning and at the end of an incubation interval. Immediately after sampling, water samples were filtered through a GF/F filter into 50 ml Falcon tubes and poisoned with HgCl₂. Later, TA was measured in duplicates via potentiometric titration with an automated titrator (Titrtrolte 7000, SI Analytics, Germany) using 25 ml of sample and 0.05 M HCl (precision ±1%). TA was calculated using the Gran approximation by determining the second endpoint of the titration curve17, and the difference in TA of the initial and final sample was used to calculate the calcification rate16. Calcification rates were related to the corresponding PAR intensities (C-I curves).

Respiration rates and dark calcification rates were derived from dark incubations. Respiration rates were added to the P-I curves. Dark calcification rates were added to the C-I curves, however corresponding to 100 μM s⁻¹ s⁻¹ (instead of 0) PAR in order to account for the delayed adjustment of calcification rates to dark conditions of about 25 min20. PAR intensity prior the dark incubation was 200–300 μM s⁻¹. A separate incubation setup was used to measure the rate of mucus release. These chambers (n = 4) consisted of acrylic cylinders (950 ml volume) equipped with a stirrer, a coral fragment holder and a Teflon membrane ‘window’ for gas exchange. They were deployed in the experimental site and filled with surrounding water. Three chambers were equipped with a coral fragment each and 1 chamber was left as a coral-free control. Incubations ran from 0900 to 1600 hrs. Three initial water samples of 1 L were collected prior to the incubations in the vicinity of the chambers and final water samples were collected at the end of the incubation period from each incubation chamber. The water samples were kept in cool boxes and filtered through pre-weighted GF/F filters in the evening of the same day. The filters were dried (60 °C) until constant weight and the carbon content was measured with a CN analyzer (Flash 2000, Thermo Scientific, Rockford, calibrated with Acetanilid) from the initial (n = 3) and final water samples (n = 1 of each chamber). Mucus release was expressed as the differences of carbon between the initial and final samples (minus the control). Only particulate carbon was measured assuming negligible rates of dissolved mucus release in Pocillopora species of the Red Sea21.

For a metabolic rate study on oxygen production (photosynthesis) and consumption (respiration) rates were converted into carbon units assuming the metabolic quotients 1.1 for photosynthesis and 0.8 for respiration20,29. Calcification and mucus release were measured as carbon precipitation (CaCO₃) and carbon release (particulate carbon), respectively. Daily rates of photosynthesis and calcification were integrated from reconstructed diurnal photosynthesis-irradiance (P-I) and calcification-irradiance (C-I) curves (Supplementary Information Fig. S1). Daily rates of mucus release were calculated assuming a 75% reduction of mucus release rates during the night and a 12:12 h day:night cycle20. Daily rates of respiration were calculated assuming enhanced respiration of 58% during the day24. For detailed description and equations for the calculation of daily metabolic rates see Supplementary Information.

Coral tissue parameters. In order to assess the effects of nutrient availability and temperature on the nutritional and energetic status of the coral, which may further influence coral growth, the coral tissue was analyzed. For this, the tissue was removed from the skeleton with a dissecting tool and an air gun. The resulting tissue slurry was homogenized (T18 basic Ultra Turrax, 10 s, 15,000 U min⁻¹), aliquoted and frozen at −20 °C for biomass and protein determination and at −80 °C for lipid analyses. Biomass was measured as the tissue dry weight, the protein concentration was determined photometrically (DU 650 Spectrophotometer, Beckman, USA) using the RCA Protein assay kit (Thermo Scientific, Rockford), and the lipid concentration was determined gravimetrically after extraction with chloroform:methanol21. Data of zooxanthellae pigmentation (photo-collecting pigments cm⁻²) were derived from a parallel study of Sawall, et al.22 on zooxanthellae of the same coral specimen. Also coral surface areas were derived from the parallel study (determined by the wax-coating method23) and used to standardize metabolic rates, mucus release and tissue parameters.

Genetic characterization. DNA extraction of the coral tissue from the same coral clades and graphically opposed to the corresponding haplotype data for a direct comparison of our data with those of Sawall, et al.22. Also genetic characterization was performed with the default settings. Data of the abundance of dominant Symbiodinium clades were derived from Sawall, et al.22, summarized by the main clades and graphically opposed to the corresponding haplotype data for a direct comparison.

Results

Biomass varied between 2.0 ± 0.2 (3-YAN summer) and 4.9 ± 0.4 mg tissue dry weight cm⁻² (2-WAJ winter) and zooxanthellae pigmentation varied between 1.8 ± 0.1 mg photosynthetically active pigments cm⁻² (5-DOG winter) and 9.6 ± 0.4 μg photo-collecting pigments cm⁻² (5-DOG winter). Both parameters, however, did not follow a latitudinal or seasonal pattern (Fig. 2c) and could consequently also not be related to changes in nutrient availability or temperature (multiple regression, Tab. 1). The protein content of the tissue was slightly higher in summer compared to winter (not significant) and rather constant throughout the sites. Minimum and maximum values were found at the most southern sites 6-FAR, with 36.5 ± 11.5% in

distinct based linear model (DistLM) was applied, since the predictor variables are not always independent of each other and partly correlate with each other. For this, a resemblance matrix based on Bray-Curtis similarity was compiled and the step-wise forward procedure with 999 permutations and the force inclusion of temperature was applied using the software Primer + PERMANOVA [PERMANOVA+ for PRIMER: Guide to software and statistical methods. Anderson, Gorley & Clarke 2008].

Correlation dued diurnal photosynthem the 6 regions (N = 79) were analysed by a hierarchical Analyses of Molecular Variance (AMOVA) in order to determine the percentage of variance explained by inter- or intra-regional variation. The principal is that the total variance is partitioned into covariance components according to inter- and intra-regional population differences, which are then used to compute the fixation index. In our case the F-statistics calculates the variation between the regional and total variation (Fₛ), for which we used Arlequin v. 3.5.1.39, taking into account the number of mutations between haplotypes. The number of haplotypes in our samples was identified using the program DnaSP v. 5.5. The phylogenetic composition of our samples as members of P. verrucosa was corroborated building a Maximum likelihood tree using MEGA V.5.34, which included all haplotypes identified in our samples together with those haplotypes from Pocillopora deposited in the Genbank data base (Pinzon et al. 2013; http://www.ncbi.nlm.nih.gov/).

| 5 : 8940 | DOI: 10.1038/srep08940 | 3 |

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summer and 14.2 ± 2.8% in winter (Fig. 2g). The lipid content was also generally higher in summer than in winter and varied between 3.2 ± 0.3% (6-FAR winter) and 9.6 ± 0.7 (4-JED summer) (Fig. 2h).

Both, protein and lipid content, correlated positively with temperature and negatively with nutrient availability (Tab. 1).

### Relationship between calcification and biological parameters

The potential effect of biogenic controls on calcification additionally to the temperature effect was tested by multiple regression (DistLM; results visualized by distance based redundancy analysis [dbRDA] as Supplementary Information Fig. S3). When testing across season and latitude, it was found that only temperature explained a significant and substantial amount of the variation in calcification (50%, Tab. 2, Fig. S3). When separating by season, it was found that in summer the protein content of the biomass and the photosynthetic rates explained an additional 26% to temperature (72%) of the variation in calcification between sites (Tab. 2). In contrast, in winter, again only temperature explained a significant part (83%) of the variation in calcification between sites.

Figure 2 | Metabolic rates (a–d) and tissue composition (e–h) of *P. verrucosa* from north (1-MAQ) to south (6-FAR) during summer (black, Sep 2011) and winter (grey, Mar 2012). Mean ± SE. Statistical results of Analysis of Covariance (ANCOVA) are presented within graphs, with S = effect of Season, L = effect of Latitude and S*L = interacting effect of Season and Latitude. Significant results are in bold.

Figure 3 | Calcification rates versus temperature. Numbers represent the mean calcification rates at prevailing temperatures for each site from north (1) to south (6) in summer (black, Sep 2011) and winter (grey, Mar 2012). The corresponding standard errors are presented in Fig. 2a. The dashed lines connect the values of the two seasons within each site.
It is undeniable that global change has taken its toll on tropical shallow water coral reefs over the last few decades, already. In particular, global warming led to losses of coral communities after major bleaching events, but also localized eutrophication and sedimentation. The question whether corals survive these changes, is a question of whether corals can adjust fast enough and/or whether corals from ‘extreme’ conditions (already adjusted) disperse fast enough to regions which become ‘extreme’ (e.g. temperatures >31°C over several weeks or even months). In order to approach these questions, we need to know first what the underlying mechanisms of adjustment are by investigating the performance and genetic constitution of corals thriving under naturally differing and extreme thermal (and nutrient) regimes. To the best of our knowledge, this is the first study investigating in situ performance and genetic composition of a tropical coral species over such a large latitudinal range (12 latitudes), and which includes naturally occurring temperatures above 31°C for several weeks or even months per year. We found strong indications for a surprisingly high phenotypic plasticity of the coral *P. verrucosa* despite large distances between reefs and strong environmental gradients in the Red Sea. This was particularly indicated by the strong temperature dependency of calcification independent of temperature history. Acclimatization rather than genetic adaptation is further supported by the low genetic divergence of the coral host from north to south.

Temperature was found to be the best explaining parameter for calcification in *P. verrucosa*, revealing a homogenous response throughout sites. This means that similar calcification rates were found at similar temperatures, independent of prevailing temperature regimes at the different sites. If we consider all Red Sea *P. verrucosa* as one population (as genetics indicate, see discussion below) then the calcification performance clearly peaks at 28–29°C. If, in contrast, we consider the local populations as distinct, then the observations that the northern populations show higher calcification rates in summer (maximum temperature), central populations show similarly high rates in summer and winter (minimum and maximum temperatures) and southern populations show higher calcification rates in winter (minimum temperatures) suggests a similar temperature response, i.e. a calcification optimum at an intermediate temperature of 28–29°C. If this would not be the case, we would expect a lower temperature dependency across sites within a given season, meaning similar calcification rates at the different sites, despite different temperatures. In any case, this homogenous response to temperature is surprising considering the low degree of overlap in temperature regimes. In the main Red Sea, there is an overlap of only 2°C between the northern reef 2-WAJ (23–30°C, annual minimum and maximum temperature) and southern reef 5-DOG (28–33°C), and there is even a gap between the temperature regimes of 1-MAQ in the Gulf of Aqaba (21–27.5°C) and 5-DOG. The strong temperature overlap of the shallow water coral reefs in our study is in contrast to the findings of Carricart-Ganivet. At the same water temperature, Carricart-Ganivet observed different calcification rates of the coral *M. annularis*, when derived from locations with different temperature regimes (Mexican Gulf: 23.5–29.5°C versus Caribbean: 26.5–29.5°C, max. distance between sites ~1000 km) and concluded that corals are adapted to regional conditions. In contrast to that, a recent study by Rodolfo-Metalpa et al. found equal temperature optima for calcification for the temperate coral *Oculina patagonica* from different regions in the Mediterranean and consequently suggested a low regional adaptation of *O. patagonica*. Compared to our study, however, his study included temperature regimes with a much greater overlap between regions, due to high seasonal temperature fluctuations (>10°C), while mean summer temperatures varied up to 3.5°C between sites (max. distance ~3000 km). Considering this, it remains remarkable that calcification of *P. verrucosa* seemingly is

**Figure 4 | Calcification-Irradiance (C-I) curves at all sites in summer (black, Sep 2011) and winter (grey, Mar 2012).** Mean ± SE (n = 3–6). Mean monthly temperatures were obtained by temperature loggers deployed over one year at the experimental site and depth. Genetic composition. A total of 7 haplotypes were identified based on the *mtORF* region, most of them present throughout the Red Sea (Fig. 5a). The genetic divergence between the regions is rather small with $F_{ST} = 0.091$ ($p = 0.015$), if followed the classification of Hartl and Clark, where $F_{ST}$-values ranging between 0.05 and 0.15 are considered as moderate genetic differentiation. This appears even smaller, if the 9.17% explained inter-regional variation is compared to the 10-fold higher explained intra-regional variation with 90.73%. Changes in the haplotype composition could not be related to changes in coral performance and tissue composition.

The *Symbiodinium* clade composition of the same coral specimens varied mainly in the most northern and most southern region. ITS2 types of clade C dominating in the Gulf of Aqaba, ITS2 type A1 was present throughout most part of the main Red Sea and the new ITS2 type A21 dominated in the very south (Fig. 5b).
Table 1 | Result of multiple regression analyses. Response variables are presented underlined, predictor variables are temperature and ‘nutrients’. Nutrients are inferred from the concentration of water chlorophyll a multiplied by the relative water flow and values are derived from Sawall, et al.16. Temperature and ‘nutrients’ are independent of each other ($r^2 = 0.16, p > 0.05$)

| Response variable: | $\beta$ | SE of $\beta$ | B | SE of B | t | p |
|--------------------|--------|--------------|---|---------|---|---|
| **Biomass cm$^{-2}$** (Adjusted $R^2 = -0.207; F(2.61) = 9.021; p = 0.000$) | | | | | | |
| Temperature | −0.118 | 0.129 | −0.048 | 0.052 | −0.921 | 0.360 |
| ‘Nutrients’ | 0.062 | 0.129 | 0.065 | 0.135 | 0.480 | 0.633 |
| **Protein, % of biomass** (Adjusted $R^2 = 0.207; F(2.61) = 9.021; p = 0.000$) | | | | | | |
| Temperature | 0.401 | 0.114 | 1.093 | 0.310 | 3.521 | 0.001 |
| ‘Nutrients’ | −0.342 | 0.114 | −2.426 | 0.808 | −3.003 | 0.004 |
| **Lipid, % of biomass** (Adjusted $R^2 = 0.566; F(2.61) = 42.152; p = 0.000$) | | | | | | |
| Temperature | 0.647 | 0.084 | 0.320 | 0.042 | 7.670 | 0.000 |
| ‘Nutrients’ | −0.522 | 0.084 | −0.671 | 0.108 | −6.207 | 0.000 |
| **Photo-collecting pigments cm$^{-2}$** (Adjusted $R^2 = -0.207; F(2.61) = 0.927; p = 0.000$) | | | | | | |
| Temperature | −0.099 | 0.130 | −0.011 | 0.151 | −0.072 | 0.943 |
| ‘Nutrients’ | 0.051 | 0.130 | 0.153 | 0.392 | 0.390 | 0.700 |
| **Mucus release cm$^{-2}$ d$^{-1}$** (Adjusted $R^2 = 0.707; F(2.61) = 77.061; p = 0.000$) | | | | | | |
| Temperature | 0.554 | 0.069 | 0.162 | 0.020 | 8.011 | 0.000 |
| ‘Nutrients’ | 0.555 | 0.069 | 0.423 | 0.053 | 8.032 | 0.000 |

Table 2 | Results of distance based linear models (DistLM). Response variable is calcification and predictor variables are temperature, mucus release, photosynthesis, biomass and % protein and % lipids of biomass. Only the best fitting models are presented

| Season: | Adj. $R^2$ | SS | Pseudo-F | p | Probability | res. df |
|---------|-----------|----|----------|---|-------------|--------|
| **September & March** | | | | | | |
| Temperature | 0.447 | 4725 | 9.880 | 0.003 | 0.497 | 10 |
| Mucus release cm$^{-2}$ d$^{-1}$ | 0.544 | 1236 | 3.135 | 0.098 | 0.130 | 9 |
| Lipids, % of biomass | 0.610 | 851 | 2.524 | 0.137 | 0.089 | 8 |
| **September** | | | | | | |
| Temperature | 0.656 | 308 | 10.538 | 0.012 | 0.725 | 4 |
| Mucus release cm$^{-2}$ d$^{-1}$ | 0.948 | 41 | 9.369 | 0.041 | 0.097 | 2 |
| Lipids, % of biomass | 0.962 | 6 | 1.802 | 0.320 | 0.013 | 1 |
| **March** | | | | | | |
| Temperature | 0.781 | 4091 | 18.879 | 0.015 | 0.825 | 4 |
| Mucus release cm$^{-2}$ d$^{-1}$ | 0.831 | 364 | 2.169 | 0.166 | 0.073 | 3 |
| Protein, % of biomass | 0.919 | 342 | 4.261 | 0.145 | 0.069 | 2 |
| Lipids, % of biomass | 0.984 | 145 | 8.973 | 0.169 | 0.029 | 1 |
Those indirect effects may additionally include processes, which are potentially competing with calcification for energy, such as the highly energy consuming mucus production. Our results revealed an overall rather weak relationship between the environmental conditions and nutritional condition of the corals. The lack of a relationship between biomass and zooxanthellae pigmentation with nutrient availability may be explained by a low capacity for heterotrophy, as suggested for this species before. The positive relationship between tissue protein and lipid content with temperatures but negative relationship with nutrient availability is not trivial. It may, however, be speculated that the increase in temperature, which increased the metabolic activity, resulted in comparatively higher burning rates of carbohydrates than of proteins and lipids and/or in a stronger built up of lipids and proteins compared to carbohydrates.

Although the concentration of photo-collecting pigments could not be related to environmental conditions, it strongly determined the photosynthetic rates, as described in the parallel study on Symbiodinium biology of P. verrucosa. In that study, a slight temperature dependency of the photosynthetic efficiency (highest between 26 and 28 °C) was found, as well. The daily photosynthetic rates, known as the main energy source, in return however, contributed only little to the explained variation in the highly energy consuming calcification rates. And mucus production, an energy consuming process and therefore potentially competing for energy with calcification, could not be related to the calcification rates at all. This is surprising considering that mucus release rates varied substantially, increasing >5-fold from north to south, where it serves as an effective defense barrier against settling dead and living particles and against increased microbial abundance and activity on the coral surface. Also the coral’s nutritional conditions contributed only little to the explained variation in calcification rates, leaving temperature as the main driver for calcification. The only additionally explained variation beside temperature was found in summer by the extreme ends of the environmental gradient in the Red Sea by promoting association of P. verrucosa with different Symbiodinium types. The different symbiont types in the north were also found to feature different physiological properties, including a higher photosynthetic efficiency and a lower seasonal regulation of chlorophyll ratios of clade C types compared to clade A. Given the particularly high calcification rates in the Gulf of Aqaba, we speculate that clade C types may also be able to translocate larger amount of photosynthetically derived energy to the host, thereby boosting calcification rates.

In summary, our study revealed a strong and largely uniform relationship of coral calcification with temperature, despite a strong shift in temperature regime (−6 °C) over the 12 degrees in latitude. Independent of latitude and season, highest calcification rates were found between 28 °C and 29 °C. This suggests a remarkable metabolic plasticity and, at the same time, little regional adaptation, as supported by the low inter-regional genetic divergence. While this may direct to a large capacity to cope with rising water temperatures due to global warming in the northern regions of the Red Sea on one hand, it suggests a limited ability to cope with global warming in the central and particularly in the southern Red Sea. This finding is supported by the high bleaching threshold found for several coral species (not only Pocillopora) in the Gulf of Aqaba in relation to prevailing temperatures, and by the observed decelerating coral growth rates in the central Red Sea as a consequence of increasing water temperatures over the last two decades. Red Sea coral genotypes featuring a high phenotypic plasticity and thermo-tolerance might therefore be able to sustain diverse and complex coral communities in the northern Red Sea during ocean warming and may even be considered as a ‘genetic reservoir’ to restock other biogeographic regions, where ocean warming decimate local coral communities. However, there seem to be upper thermal limits for
physiological performance and as adaptation, considering that corals originating from the central and southern Red Sea perform better at ‘cold’ winter temperatures than at ‘hot’ summer temperatures.

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Acknowledgments
We thank the accompanying divers N. Marimuthu, S. Al-Abahi, A. Gokhari, F. Schuster, C. Lieberum, B. Hoang, our boat driver A. Al-Hamed and the Saudi Arabian coast guard. We also thank the Bioscience Core Lab at KAUST for sequencing. We are grateful for helpful comments on the manuscript from C. Richter. This project was funded by KAU and GEOMAR (Germany). Further support was provided by KAUST (Saudi Arabian Academic Excellence Alliance Award 1000000853) and GOEMAR (Germany).

Data availability
See the data availability platform PANGAEA (www.pangaea.de) under doi.pangaea.de/10.1594/PANGAEA.841401.
Author contributions
Y.S., A.A.-S. and M.W. designed the study. Y.S., A.A.-S. conducted the in situ metabolism and coral tissue measurements. E.B.-H. and C.R.V. conducted the genetic analyses. S.H. reconstructed the C-I and P-I curves and calculated the carbon budget. Y.S., M.W., S.H. and C.R.V. wrote the manuscript. All authors reviewed the manuscript.

Additional information
Supplementary information accompanies this paper at http://www.nature.com/scientificreports

Competing financial interests: The authors declare no competing financial interests.

How to cite this article: Sawall, Y. et al. Extensive phenotypic plasticity of a Red Sea coral over a strong latitudinal temperature gradient suggests limited acclimatization potential to warming. Sci. Rep. 5, 8940; DOI:10.1038/srep08940 (2015).

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