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With ongoing climate change, coral susceptibility to thermal stress constitutes a central concern in reef conservation. In the Persian Gulf, coral reefs are confronted with the most extreme temperatures. Over the last decades, both annual hot and cold peak periods in this region have been associated with episodes of coral bleaching and mortality. Using physiological performance as a measure of coral health, we investigated the thermal susceptibility of the common acroporid coral from the Persian Gulf, *Acropora downingi*, in Hengam Island where temperature oscillates seasonally in the range 20.2-34.2°C. In a series of two short-term experiments, we exposed corals (1) to the constant temperature levels of summer versus winter, and (2) to progressive temperature deviations from the annual mean toward the two extreme seasonal values and beyond. We monitored four indictors of coral physiological performance: net photosynthesis (Pn), dark respiration (R), autotrophic capability (Pn/R), and survival. Warming revealed detrimental for Pn and survival of corals, while equivalent cooling did not. Pn/R was lower at the warmer thermal level within each season, and during summer compared to winter. Corals exposed to the maximum temperature of summer displayed Pn/R<1, inferring that photosynthetic performance could not support basal metabolic needs under this environment and that corals had to import organic matter or draw on their reserves to compensate for carbon losses during respiration. We therefore suggest that the Persian Gulf populations of *A. downingi* are more sensitive to the extreme temperatures endured in summer compared to that experienced in winter; and they may be impacted by future increases in water temperature.

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Abstract

With ongoing climate change, coral susceptibility to thermal stress constitutes a central concern in reef conservation. In the Persian Gulf, coral reefs are confronted with the most extreme temperatures. Over the last decades, both annual hot and cold peak periods in this region have been associated with episodes of coral bleaching and mortality. Using physiological performance as a measure of coral health, we investigated the thermal susceptibility of the common acroporid coral from the Persian Gulf, *Acropora downingi*, in Hengam Island where temperature oscillates seasonally in the range 20.2-34.2°C. In a series of two short-term experiments, we exposed corals (1) to the constant temperature levels of summer versus winter, and (2) to progressive temperature deviations from the annual mean toward the two extreme seasonal values and beyond. We monitored four indictors of coral physiological performance: net photosynthesis (Pn), dark respiration (R), autotrophic capability (Pn/R), and survival. Warming revealed detrimental for Pn and survival of corals, while equivalent cooling did not. Pn/R was lower at the warmer thermal level within each season, and during summer compared to winter. Corals exposed to the maximum temperature of summer displayed Pn/R<1, inferring that photosynthetic performance could not support basal metabolic needs under this environment and that corals had to import organic matter or draw on their reserves to compensate for carbon losses during respiration. We therefore suggest that the Persian Gulf populations of *A. downingi* are more sensitive to the extreme temperatures endured in summer compared to that experienced in winter; and they may be impacted by future increases in water temperature.

Key words: coral reefs, global warming, Persian Gulf, seasonal performance, thermal tolerance.

Introduction

Extreme deviations in water temperature negatively affect physiological performance of scleractinian corals during both cold and warm seasons (Saxby et al. 2003; Roth et al. 2012; Roth & Deheyn 2013), causing widespread coral bleaching and mortality, and threatening tropical reefs (Hoegh-Guldberg et al. 2005; Lirman et al., 2011; Eakin et al. 2008). Thermal tolerance is however variable from one coral species to another and among regions (Jokiel & Coles 1990; Marshall & Baird 2000), and the assessment of thermal susceptibility of major reef-building corals from multiple regions are therefore research priorities to evaluate vulnerability of reef ecosystems to climate change. Coral reefs from the Persian Gulf subsist in a singular highly oscillating environment that in the summer constitutes the world's warmest sea, and in the winter one of the coldest seas hosting coral reefs (Kleypas et al. 1999; Sheppard et al. 2010). Therefore, estimating the thermal sensitivity of Persian Gulf corals is not only important for a more effective reef conservation in the region, but will also benefit our general understanding of the ability of corals to adapt or acclimate to temperature variations (Feary et al. 2013).

Coral sensitivity to seasonal temperature variations has been estimated on some southern Persian Gulf reefs by recording thermal thresholds at occurrences of bleaching events. In this regard, *Acropora* bleaching was associated with 3 weeks of exposure to >35°C average daily temperatures in summer (Riegl et al. 2012), and with more than 4 weeks of exposure to <13°C average daily temperatures in winter (Coles & Fadlallah 1990). Thermal threshold of bleaching however does not give much information about the effects of the non-bleaching range of temperature on physiological performance of corals, and cannot be generalized to reef areas where records of water temperature and bleaching events are scarce.

Here, we experimentally evaluated the effects of seasonal temperature variations on physiological performance of a common acroporid coral from Hengam Island, northeastern Persian Gulf, where no fatal coral bleaching has ever been documented (Vajed Samiei et al. in press). In a series of two short-term experiments, we exposed branchlets of *Acropora downingi* to (1) constant mean summer versus winter temperatures, and (2) progressive deviations from the annual mean temperature toward seasonal thermal extremes, and evaluated coral physiological response by measuring net photosynthesis (Pn), dark respiration (R), net photosynthesis to respiration ratio (Pn/R), and survival. Our results indicate that autotrophic ability of *A. downingi* is higher at winter thermal levels compared to summer conditions, and that this species is more sensitive to the positive annual extreme temperatures encountered during summer compared to winter minima.

Materials and methods

Sampling site and procedure

The study consisted in two sets of complementary short-term experiments conducted in summer and winter 2012-13 on Hengam Island, located in the northeastern section of the Persian Gulf. Hengam reef is washed by water currents coming through the Strait of Hormuz from the Oman Sea and hence experiences milder seasonal water temperatures compared to reefs situated more inward in the Persian Gulf. The minimum, mean and maximum annual water temperatures at our sampling site are respectively 20.2, 27.5 and 34.2 °C; and the mean daily water temperatures during the warm and cold seasons are respectively 32.4 and 21.6°C (Vajed Samiei et al. in press). During the warm season, tidal flows frequently impose short-term temperature variations as big as 5.5°C in the course of 1 to 3 h to the Hengam coral community (Vajed Samiei et al. in press).

We used *Acropora downingi* as a study model, as it dominates coral patches of Hengam Island and is one of the major reef-building corals in the Persian Gulf (Rahmani et al. 2013). Experiments were performed on a daily basis on two 10-15 cm branches of *A. downingi* collected from a depth of about 4 m and transported in seawater and low light condition to the nearby laboratory by 15 min. Samples were kept immersed in 27.5°C aerated seawater for 3 h prior to experiments.

Experimental set up and measurements

Physiological performance of corals was evaluated using the oxygen anomaly technique in a closed, temperature-regulated aquarium as illustrated in Figure 1. This technique has the advantage of not being affected by micro-scale variability of photosynthetic activity along surfaces and can be used for estimating net metabolic performance of coral colonies or other macro-photosynthetic organisms (Maxwell & Johnson 2000; Levy et al. 2004).

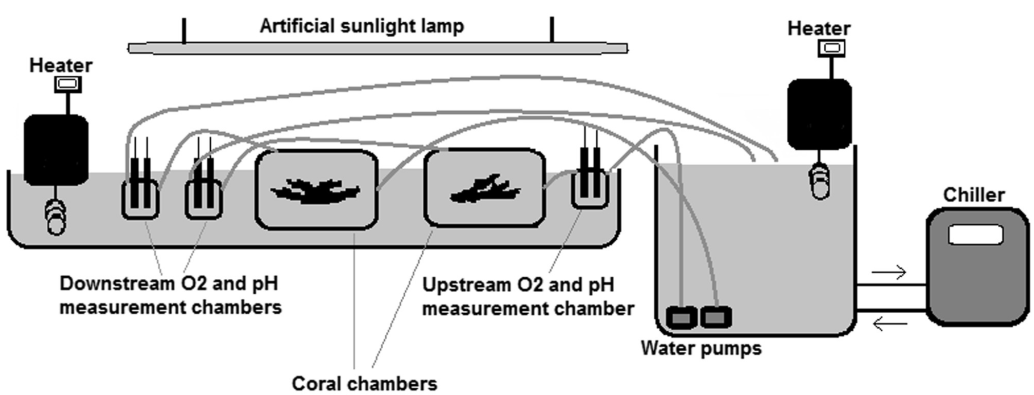

Figure 1. Experimental set up. Seawater collected from the study site was pumped through the system at a constant rate of about 0.5 $l.min^{-1}$. Oxygen concentration ($mg.l^{-1}$) and pH were recorded upstream and downstream the coral chambers every 5 minute. ~6500 lux light was provided by an artificial sunlight lamp (Dymax Rex-2). Water temperature was controlled by heaters (Lauda E100, with accuracy of ± 0.1°C) and a chiller (Aqua medic Titan 1500, with accuracy of ± 0.5°C). Net photosynthesis or respiration rate of corals was calculated in light and dark conditions as the difference in O_2 concentration between the upstream and downstream chamber.

Prior to experiments, the system was filled with seawater and run for about 2 h until no difference in upstream and downstream waters was observed. Through experiments, O_2 concentrations ($mg.l^{-1}$) in upstream and downstream chambers were simultaneously logged every 5 min using dissolved oxygen loggers (HACH, IntelliCAL™ LDO101 luminescent/optical dissolved oxygen). Oxygen exchange was calculated by subtracting the downstream O_2 concentration from the upstream value, and was referred as net photosynthesis (Pn) when positive as corals were exposed to light, and as dark respiration (R) when negative as corals were kept in the dark.

Light intensity was kept constant and approximate to 6500 lux (supplementary data). In summer, the average day light intensity at Hengam coral community was 6679 ± 6503 SD and 4242 ± 3587 SD at depths of ~3m and 6m (supplementary data). Water was flowing into the system with a velocity of 66 $cm.s^{-1}$, and hence well mixed inside the coral chambers. Water pH was maintained higher than 8 by renewing a constant volume of the source water during the experiments (20 l per 3 h). After experiments, surviving corals were transplanted back to the sampling site on natural hard substrate or concrete blocks. Living status of transplants was examined subsequently for few months.

Experiment one: exposure to average and peak seasonal temperatures

In each season, coral specimens (n = 3-6) were consecutively exposed to 2.5 h periods of light and darkness at the corresponding mean and peak temperatures: respectively 23°C and 20.2°C in winter, versus 32°C and 34.2°C in summer. For each combination of temperature and light, Pn or R was calculated by averaging oxygen exchange over the last hour of exposition. Net photosynthesis to dark respiration ratio (Pn/R) was calculated as a proxy to autotrophic capability of corals. Indeed, Pn/R ≥ 1 infers the coral is potentially photoautotrophic with respect to carbon and does not require external supply, while Pn/R < 1 indicates that carbon must be acquired from other nutritional sources (McCloskey et al. 1978). Pn, R and Pn/R of corals were compared between thermal levels within each season (i.e. seasonal mean vs. seasonal peak) using t-test for dependent samples in Statistica 8 software. Pn/R ratio was compared between respective thermal levels of the two seasons (i.e. summer mean vs. winter mean and summer peak vs. winter peak) using t-tests for independent samples in Statistica 8.

Experiment two: exposure to gradual deviation toward seasonal temperature extremes

Coral specimens (n = 5) were exposed to gradual deviation in water temperature from the mean annual level of 27.5°C (temperature of reference, dT = 0°C) toward the seasonal extremes of 38°C in summer and 17°C in winter (|dT| = 10.5°C). Temperature was varied at a consistent rate of 0.2°C per 10 min. This rate is representative of temperature variations as frequently experienced by coral communities on Hengam reefs (Vajed Samiei et al. in press) and has been widely used in experimental studies to assess thermal tolerance of corals and other animals (Brown & Cossins 2011). Variation in coral net photosynthesis was compared among treatments using Linear Mixed-effect Models (LMMs). LMMs are appropriate for analyzing longitudinal data via correction for temporal autocorrelation, and allow taking into account inter-subject variability via the specification of random effects in the model (Pinheiro et al. 2008). Difference in Pn to dT profiles of corals among heating and cooling experiments were established using a modern semi-parametric contrast curve approach combining LMMs and penalized splines (see Ruppert et al. 2003; Durbán et al. 2005; Kayal et al. in review for mathematics and programming syntax). LMMs and contrasts were computed in R software (R Development Core Team 2008) supplemented by NLME (Pinheiro et al. 2008) and BRugs (Ruppert et al. 2003) packages. Prior to LMMs, the relationship between Pn and dT was linearized by the square transformation of dT to satisfy normality requirements. All statistical analyses were performed at a confidence level of 95%.

Results

Experiment one: exposure to average and peak seasonal temperatures

Coral net photosynthesis was relatively consistent between the seasonal peak and mean thermal levels of winter (0.24 ±0.04 versus 0.26 ±0.06 SE mg O_2 respectively), while it was considerably lower at the seasonal peak compared to the mean temperature in summer (0.11 ±0.03 versus 0.24 ±0.06 SE mg O_2 respectively, Table 1). Coral respiration was highest at the warmer thermal level within each season. The net photosynthesis to dark respiration ratio Pn/R decreased with temperature both within and between seasons, although it did not differ significantly between winter thermal levels (Table 1).

Table 1. Results of the t-test for dependent samples comparing the magnitude of Pn, R and Pn/R of corals between thermal levels of each season (i.e. summer mean vs. summer peak and winter mean vs. winter peak), and t-tests for independent samples comparing Pn/R ratio between equivalent thermal levels of two seasons (i.e. summer mean vs. winter mean and summer peak vs. winter peak).

		Summer (n=6)		Winter (n=3)		
	Experimental water temperature	**Mean**	**SE**	**Mean**	**SE**	
Pn	Average of the season (32 or 23°C)	0.24	0.05	0.26	0.06	
	Peak of the season (34.2 or 20.2°C)	0.11	0.03	0.24	0.04	
	Pairwise comparison	t-value=4.09* p<0.01		t-value=0.80 p>0.05		
R	Average of the season	-0.21	0.03	-0.13	0.05	
	Peak of the season	-0.27	0.02	-0.08	0.04	
	Pairwise comparison	t-value=-3.84* p<0.05		t-value=-4.83* p<0.05		**Pairwise comparison**
Pn/R	Average of the season	1.05	0.07	1.86	0.12	t-value=-6.01* p<0.001
	Peak of the season	0.39	0.07	2.83	0.40	t-value=-8.72* p<0.0001
	Pairwise comparison	t-value=15.83* p<0.0001		t-value=2.59 p>0.05		

All specimens survived exposition to the thermal levels tested during the experiments, and no sign of stress was observed one week and six months after transplantation back in the natural environment.

Experiment two: exposure to gradual deviation toward seasonal temperature extremes

Coral net photosynthesis Pn was differently affected by positive versus negative temperature deviations (LMM, interaction *Treatment* × dT^2, $p < 0.001$). Pn remained relatively consistent when water temperature was lowered from the annual mean value of 27.5°C toward a minima of 17°C (estimated Pn of 0.25 ±0.03 and 0.21 ±0.02 SE mg O_2 respectively), but decreased substantially with equivalent positive deviation toward a maxima of 38°C (estimated Pn of -0.07 ±0.02 at 38°C; Figure 2). Net photosynthesis was reduced by 50% at the summer maxima level of 34.2°C (estimated Pn of 0.12 ±0.03 mg O_2), and was negative above a temperature of 36.8°C (dT=+9.3°C). Coral photosynthetic performance differed significantly between heating and cooling treatments for a temperature deviation |dT|>1.3°C (dT^2>1.6°C, see contrast curve in Figure 2).

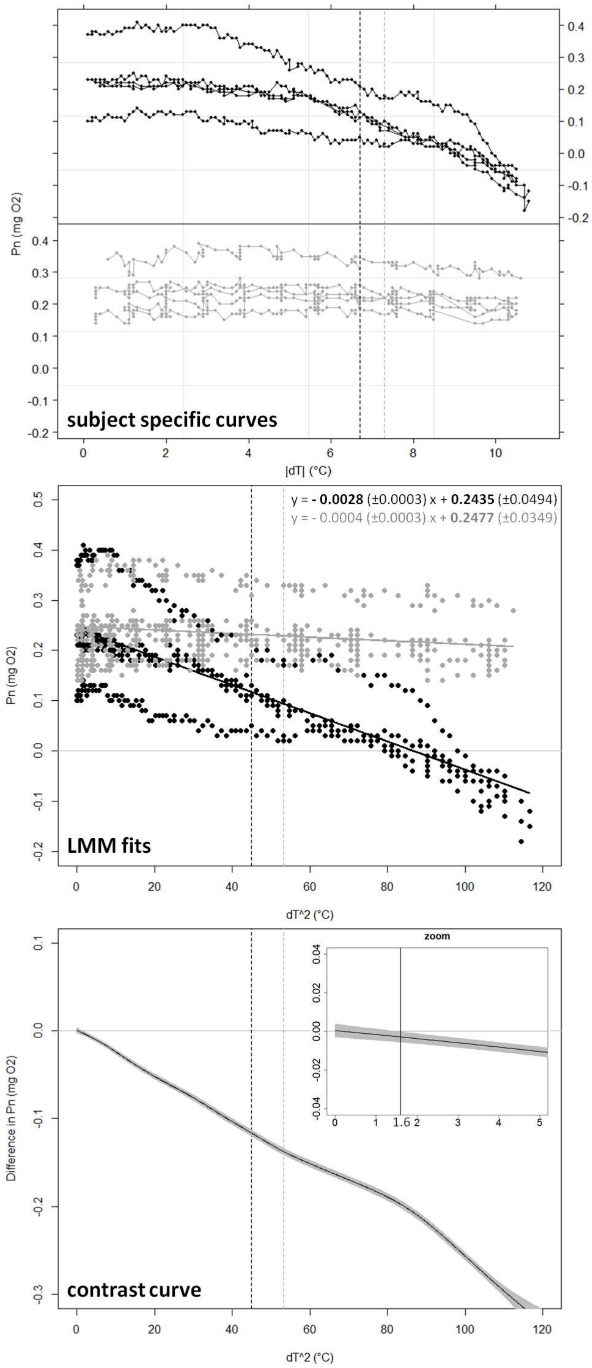

Figure 2. Coral net photosynthesis Pn as a function of positive (black) versus negative (grey) temperature deviation |dT| from the annual mean value of 27.5°C. Top graph shows raw data as recorded for each of the n=5 replicate coral fragments within each treatment. The graph in centre shows the fit from the Linear Mixed-effect Model (LMM) in the linearized dimension ($x=[dT]^2$). The equations of the linear regressions are provided in the form *y* = *slope* (±SE) *x* + *intercept* (±SE), and significant equation parameters are printed in bold character. Bottom graph illustrates results from the semi-parametric contrast curve (based on LMM and penalized splines) identifying the domain of significant difference between the two profiles: the curves are significantly different when the contrast curve ±CI (black-line ±shading) does not overlap with the y=0 line (here for $[dT]^2$>1.6°C or dT=1.3°C; see vertical line in zoom insert). Black and grey dashed lines indicate the levels of the peak temperatures observed at the study site in summer (34.2°C) and winter (20.2°C) respectively.

Positive temperature deviations toward summer extremes revealed fatal for corals while equivalent negative deviations toward winter minima did not. No sign of stress was observed on surviving coral specimens one week and six months after transplantation back in the natural environment.

Discussion

Increasing evidence of climate change toward a warmer environment has set great emphasis on the importance of assessing thermal susceptibility of corals in reef conservation (Berkelman 2002). In a set of two complementary short-term experiments, we exposed fragments of the common reef coral *Acropora downingi* from Hengam Island, Persian Gulf, to water temperature levels as encountered in the natural environment in summer and winter, and recorded coral physiological activity. Results of both experiments indicate that the summer positive thermal deviations are more detrimental for physiological performance and survival of *A. downingi* than winter negative thermal deviations. Coral net photosynthesis was negatively affected by elevation in water temperature from the annual mean level of 27.5°C, was reduced by half at the summer maxima of 34.2°C, and became negative beyond 36.8°C (i.e. higher O_2 consumption via respiration than production via photosynthesis). Besides, corals exposed to 38°C did not survive. In contrast, no significant variation in photosynthetic performance and survival was observed facing above 10°C decline in temperature. Similarly, the balance between net photosynthesis and dark respiration displayed by the Pn/R ratio was lower at summer thermal levels compared with winter ones. Corals are considered autotrophic when the Pn/R ratio is > 1, and since proportion of algal photosynthate which is translocated to the host coral polyp might vary from 35 to 90 percent in different species of corals (Muscatine et al. 1984; Tremblay et al. 2012), a Pn/R ratio of ~2 is usually considered representative of a good coral condition; i.e. where the zooxanthellae is supplying the basal metabolic requirements of the polyp (McCloskey et al. 1978). Our results (see Table 1) suggest *A. downingi* is autotrophic during winter but loses its capability to sustain its energetic demands through photosynthesis at warmer summer thermal levels. This pattern concords with findings by Coles & Jokiel (1977) who showed that Pn/R ratios were decreasing with increasing temperature in several Hawaiian scleractinian corals over their natural temperature range. In contrast with tropical and subtropical corals, Pn/R ratios of temperate corals are more sensitive to the lower range in ambient temperature (Nakamura et al. 2004; Rodolfo-Metalpa et al. 2010).

Our findings suggest that *A. downingi* populations around Hengam Island are living closer to their superior thermal threshold and thus would be more affected by a warmer climate, or by occurrences of extreme summer events compared to harsher winters. This notably explains why the majority of *Acropora* bleaching events in the highly oscillating thermal environment of the Persian Gulf have occurred during positive temperature anomalies (Riegl 2002; Sheppard & Loughland 2002; Riegl 2003; Burt et al. 2008; Riegl 2011), while few bleachings followed negative thermal stresses (Shinn 1975; Coles & Fadlallah 1990). Current projections under RCP (Representative Concentration Pathways) 8.5 predict that seawater temperature increase by 4.26°C over 2010-2099 in the Persian Gulf (Hoegh-Guldberg et al. 2014). In the current study, coral photosynthetic performance diverged between heated and cooled environments above a thermal deviation of 1.3°C from the annual mean level, and was rapidly depressed by further temperature increases. *A. downingi* did not survive exposition to a temperature 3.8°C higher than the peak summer level as experienced in its natural environment. Therefore, in absence of significant adaptation, forthcoming increase in water temperature may strongly impact *A. downingi* populations of the Persian Gulf. Corals of the Persian Gulf experience water temperatures that in summer are close to the thermal levels many tropical coral reefs are expected to face by the end of the century (Riegl et al. 2012). Understanding their physiological performance and susceptibility may provide valuable insights about the adaptation and acclimation capability of reef corals.

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