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**Title:** Differential thermal tolerance between algae and corals may trigger the proliferation of algae in coral reefs

**Running title:** Thermal tolerance of algae and coral species

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## Abstract

Marine heatwaves can lead to rapid changes in entire communities, including in the case of shallow coral reefs the potential overgrowth of algae. Here we tested experimentally the differential thermal tolerance between algae and coral species from the Red Sea through the measurement of thermal performance curves and the assessment of thermal limits. Differences across functional groups (algae vs corals) were apparent for two key thermal performance metrics. First, two reef-associated algae species (*Halimeda tuna* and *Turbinaria ornata*,) had higher lethal thermal limits than two coral species (*Pocillopora verrucosa* and *Stylophora pistillata*) conferring those species of algae with a clear advantage during heatwaves by surpassing the thermal threshold of coral survival. Second, the coral species had generally greater deactivation energies for net and gross primary production rates compared to the algae species, indicating greater thermal sensitivity in corals once the optimum temperature is exceeded. Our field surveys in the Red Sea reefs before and after the marine heatwave of 2015 show a change in benthic cover mainly in the southern reefs, where there was a decrease in coral cover and a concomitant increase in algae abundance, mainly turf algae. Our laboratory and field observations indicate that a proliferation of algae might be expected on Red Sea coral reefs with future ocean warming.

**Key words:** Heatwaves, Red Sea, thermal limits, turf algae, thermal vulnerability

## Introduction

In the past century, global rise in ocean temperatures has led to longer and more frequent marine heatwaves - prolonged periods of anomalously high temperature - and in the last decade the ocean has reached the warmest temperatures ever observed (Coumou & Rahmstorf, 2012; Oliver et al., 2018). The projection is that the average duration of marine heatwaves (in days) will increase by a factor of 16 for global warming of 1.5 °C and by a factor of 23 for global warming of 2 °C relative to preindustrial levels (Frölicher et al., 2018). Marine heatwaves can exert devastating impacts on ecosystems (Normile, 2016; Oliver et al., 2017), such as the widespread mortality of Mediterranean soft corals and seagrasses (Marbà et al., 2015; Marbà & Duarte, 2010) reported during the 2003 European heatwave. Similarly, the 2011 marine heatwave off

Western Australia caused the replacement of kelp forests with seaweed turfs (Wernberg et al., 2016) and widespread seagrass mortality (Arias-Ortiz et al., 2018).

Heatwaves are also propelling the global degradation of already distressed coral reefs by triggering mass coral bleaching and vast die-offs (Hughes et al., 2018). For example, the global 2015/2016 heatwave, associated with an El Niño event, caused widespread mortality of coral reefs in the Indo-Pacific region (Hughes et al., 2018). In some instances, the decline in coral cover occurs concurrently with the proliferation of algae (Roff et al., 2015), and can, in extreme cases, result in a community shift from coral- to algae-dominated states (Graham et al., 2015; Hughes, 1994). The Greater Caribbean Basin has experienced a dramatic loss of coral cover and an increase in algae cover (Aronson & Precht, 2001; Hughes et al., 2003) - an isolated or compound effect of eutrophication, coral disease outbreaks, hurricanes, ocean warming and the decline of herbivores. In the Indo-Pacific, the proliferation of algae are seemingly less common (Bruno et al., 2009), but have been reported in some locations after severe coral mass-mortality events (Graham et al., 2015).

The role of ocean warming and heatwave events in changing the abundance of algae within coral reefs has been poorly studied (Bridge et al., 2014), despite expectations of algae to either benefit from increasing temperatures or remain relatively unaffected (Brown et al., 2019; Hoegh-Guldberg, 1999; Hughes, Graham, Jackson, Mumby, & Steneck, 2010, but see Bender-Champ, Diaz-Pulido, & Dove, 2017). Experimental studies report that the upper thermal limits of corals are linked to geographic location and the thermal range experienced under ambient conditions (Coles & Brown, 2003). Reported thermal thresholds for coral bleaching and mortality range 8-10 °C worldwide: from 27 °C in Rapa Nui (with a summer ambient maximum of 25°C; Wellington et al., 2001) to 35-37 °C in the Arabian Gulf (Coles & Riegl, 2013), where the summer ambient mean maximum is 34-35 °C (Riegl et al., 2012). Therefore, during summer months corals are exposed to mean maximum temperatures that are typically 2 °C below their upper thermal limits, such that heatwaves leading to a warming of > 2 °C can have catastrophic consequences. Ocean warming can also induce extensive benthic algae mortality (Phelps et al., 2017), which has been mostly reported for the low-latitude biogeographical boundary of temperate kelps (Filbee-Dexter et al., 2016; Wernberg et al., 2016), but has not yet been reported for tropical algae. Indeed, we are aware of just a single experimental assessment of the upper thermal lethal limit of tropical benthic algae (Anderson, 2006), reporting the lethal temperature

thresholds for six species of algae in the Florida Keys, where the mean maximum temperature was approximately 31 °C (Jaap et al., 2008; McMurray et al., 2011). Anderson (2006) reported lethal thermal limits ranging from approximately 33 °C for three species to > 34 °C for the other three algae species tested (lethal thermal limits estimated from Table 4 in Anderson 2006). Therefore, 50% of the algae were, along with the corals, growing at a mean summer maximum water temperature of approximately 2 °C below their lethal thermal limits, while the other algae species were more thermo-tolerant (lethal thermal thresholds >3 °C above the mean summer maximum water temperature). Nonetheless, to date, few studies assess the thermal performance of corals and algae from the same geographic location (Brown et al., 2019), and none have compared lethal thermal limits in combination with thermal performance curves between coral and algae, which may reveal differential vulnerability towards a warming ocean.

Thermal performance curves (TPCs) characterize organismal physiological rates of performances across the thermal range they tolerate (Fig. S1). They are typically unimodal and asymmetric (Aichelman et al., 2019; Huey & Kingsolver, 1989; Kingsolver, 2009; Savva et al., 2018), meaning that performance slowly rises at a rate indicated by the activation energy ( $E$ ) until a maximum rate is reached at the optimal temperature ( $T_{opt}$ ). A decline in performance follows the  $T_{opt}$  and the abruptness of this fall is represented by the slope of the activation energy in the falling side of the curve ( $E_h$ ; Padfield, Yvon-Durocher, Buckling, Jennings, & Yvon-Durocher, 2016). A critical maximum temperature ( $CT_{max}$ ) is reached at very low individual performance rates (Silbiger, Goodbody-Gringley, Bruno, & Putnam, 2019), and, ultimately, a lethal threshold is reached. This lethal threshold is usually quantified empirically at the population level with mortality curves that assign the thermal limit when 50% mortality of individuals (e.g.,  $TL_{50}$ ) is reached. Therefore, parameters obtained from thermal performance curves (e.g.,  $T_{opt}$ ,  $CT_{max}$ ,  $E$ , and  $E_h$ ) in combination with mortality curves (e.g.,  $TL_{50}$ ) provide key comparable information about species response and sensitivity to heat stress and warming.

We propose and test three potential and not mutually exclusive thermal-performance theoretical scenarios providing a competitive physiological advantage of tropical algae over coral species under heat stress. First, we consider a theoretical scenario where the  $T_{opt}$  and  $LT_{50}$  of tropical algae species are higher than that of coral species (M3 on Fig. S1), providing algae with an advantage in their thermal performance and survival during heatwaves. In a second scenario, coral and algae species may have similar  $T_{opt}$  but algae may have a higher  $LT_{50}$  (M2 on Fig. S1),

favoring algae performance and survival at temperatures above the  $T_{opt}$ . In a third scenario, algae would have lower  $T_{opt}$  but higher  $LT_{50}$  than corals (M1 on Fig. S1), providing corals with a higher competitive ability as they approach their  $T_{opt}$ , but algae being more resistant to rising temperatures after the coral survival threshold (e.g.,  $LT_{50}$ ) is surpassed.

Here we tested the theoretical scenarios above by experimentally assessing thermal performance and mortality curves for three common algae species and two coral reef-building species in the Red Sea. Thereafter, we examined the consistency between the expectations from the experimental results and observed changes in the benthic community before and after a heatwave. The 2015/2016 heatwave triggered the longest and most widespread Indo-Pacific coral bleaching event on record (Hughes et al., 2017), and affected the Red Sea in the summer/fall of 2015 (Hughes et al., 2017; Monroe et al., 2018; Osman et al., 2018), where coral bleaching was restricted to the central and southern regions, and intensified southward (Monroe et al., 2018; Osman et al., 2018). We performed large-scale quantitative field surveys during 2017-2019, spanning >1,000 km along the Red Sea coastline, reporting the benthic status of coral reefs (i.e., live coral and algae % cover) after this record-breaking global heatwave and contrasted these results with surveys conducted in 2014-2015 before the heatwave (Ellis et al. 2019).

## **Materials and methods**

### **Thermal performance curves**

The experimental response of five key species of benthic organisms to a thermal regime was assessed in the fall of 2016 in the Red Sea. Specimens were collected from Alfahal Reef, a shallow coral reef in the central Red Sea, in November of 2016 (22.25834N, 38.96222E). The targeted species are commonly found in coral reefs along the Red Sea: a calcareous green algae (*Halimeda tuna*), a fleshy brown algae (*Turbinaria ornata*), an encrusting calcareous red algae (*Lithothamnion* sp.), a thermally-resistant reef-building coral (*Stylophora pistillata*) and thermally-sensitive reef-building coral (*Pocillopora verrucosa*). Specimens were maintained in holding tanks at the marine research facility CMOR (KAUST) with continuous flowing raw seawater on a light:dark (12h:12h) cycle and at a constant level ( $140 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ ) of photosynthetically active radiation (PAR). All specimens were acclimated in the tanks for 10 days at 28 °C until the beginning of the experiment.

The targeted temperatures for taking measurements were: 28, 30, 32, 34, 36 and 38 °C, in order to encompass the upper thermal niche of the selected species and their lethal thermal thresholds. The mean temperatures achieved during the experiment were within 0.5 °C from the targeted temperatures (Table S1). Temperatures were gradually increased using underwater thermometers (SCHEGO Schemel & Goetz GmbH & Co, Germany) in 3 large holding tanks (240 liters) by 1 °C per day for two consecutive days and then maintained for two additional days at the targeted temperatures. Incubations in 2 L experimental glass jars were performed on those two days. The total duration of the experiment was 22 days. Controls were conducted (n=2 for each species) at 28 °C and no mortality and/or bleaching was detected for any specimens. Metabolic rates (e.g., gross primary production - GPP, respiration - R, and net production - NP) were assessed on individual specimens enclosed carefully in the glass jars in which a miniDOT sensor (Precision Measurement Engineering, Inc, USA) recorded dissolved oxygen and temperature for at least 2 hours at each targeted temperature. Incubations of the jars were performed in Percival incubators (Percival Scientific, Inc, USA) at a PAR of 120 and 0  $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$  for the light and dark period, respectively. A total of 20 jar incubations were performed at each targeted temperature (n=4 replicates for each species at each targeted temperature). The surface area of corals and algae were calculated by taking videos, extracting pictures of each specimen from 120 different angles to create a properly scaled 3-dimensional digital image and analyzing them with ReMAKE software (Autodesk, USA; Fig. S2). The metabolic rates for each incubation were normalized to the surface area of the corresponding algae or coral fragment (Aichelman et al., 2019), and expressed in  $\mu\text{mol O}_2 \text{ cm}^{-2} \text{ h}^{-1}$ .

Thermal performance curves for each metabolic rate (e.g., GPP, R and NP) were quantified by fitting the four parameter Sharpe-Schoolfield equation to the rate (the mean of four replicates per species was calculated at each temperature) measured along the thermal gradient for each species (Padfield et al., 2016, 2017):

$$\ln(r(T)) = E (1/kT_c - 1/kT) + \ln(r(T_c)) - \ln(1 + e^{E_h(1/kT_h - 1/kT)}) \quad [1]$$

where  $r(T)$  is the metabolic rate ( $\mu\text{mol O}_2 \text{ cm}^{-2} \text{ h}^{-1}$ ),  $k$  is Boltzman's constant ( $8.62 \times 10^{-5} \text{ eV K}^{-1}$ ),  $E$  is the activation energy (eV) up to a thermal optimum,  $T$  is temperature (K),  $T_h$  is the temperature where half the enzymes are rendered non-functional,  $E_h$  characterizes temperature-induced deactivation energy of growth above  $T_h$ , and  $r(T_c)$  is the metabolic rate normalized to a reasonable reference temperature ( $T_c = 28 \text{ °C}$ ), where no low or high temperature inactivation is

expected to be experienced. Equation [1] yields a maximum metabolic rate at an optimum temperature as follows:

$$T_{opt} = E_h T_h / (E_h + k T_h \ln (E_h / E - 1)) \quad [2]$$

We did not achieve near-zero respiration (R) rates in any of the species, making the calculation of the parameters of the thermal performance curve unfeasible. Therefore, respiration rates are only presented in the supplementary material (see Fig. S3).  $CT_{max}$  was defined as the temperature at which there was a 90% loss of the maximum rate at  $T_{opt}$  (Silbiger et al., 2019).

We also calculated the temperature at which organismal productivity switched from net autotrophic to net heterotrophic ( $T_{np=0}$ ), as the intercept of the fitted thermal performance curve for net production (NP) with temperature (i.e. temperature at which NP = 0). NP > 0 sets the domain where both algae and corals can support viable populations, where their autotrophic production is sufficient to meet their metabolic demands (i.e., NP = 0), and generate organic carbon surplus to support growth, reproduction and losses (NP > 0). Whereas the requirement for NP > 0 for algae to remain viable is straightforward, that for scleractinian corals, which supplement their carbon budget through phagotrophy and ciliary feeding, is less evident. However, NP < 0 compromises both the supply of organic carbon to support coral growth and reproduction as well as the oxygen balance of the holobiont, as the photosynthetic oxygen produced is used to support the polyp respiration (Kühl et al., 1995), while removal of CO<sub>2</sub> through coral photosynthesis helps support conditions conducive to polyp calcification (Kühl et al., 1995). Indeed, coral bleaching represents a decline in symbiont density, and NP, depleting the autotrophic potential of coral metabolic balance, which often leads to coral mortality.

### **Lethal thermal limits**

The mortality of specimens was recorded daily, which allowed for calculating % mortality at 1 °C increments in temperature, after correcting for the abundance of individuals. The mortality of individuals was determined: for the coral, by a rapid loss of live tissue (which included observable loss of polyps), for *Lithothamnion* sp., an intense whitening, for *T. ornata* a withering and loss in tissue turgidity, and for *H. tuna*, an increase in tissue rigidity and paling tissue coloration. Dead individuals were immediately removed from the experimental tanks, and the experiment was terminated when 38 °C was achieved. The lethal thermal limit of organisms

( $LT_{50}$ ), defined as the temperature causing 50% mortality in a given species, was estimated using the log-logistic two parameter dose-response model (Ritz et al., 2015):

$$\text{Mortality (\%)} = 100 / (1 + a (\log(T) - \log(LT_{50}))) \quad [3]$$

where  $a$  is the slope of the dose-curve and lower and upper asymptotes of the response were set at 0 and 100% mortality, respectively.

### Quantitative field observations

Field observations at 35 coral reef sites were performed along the coast of the Red Sea (Saudi Arabia) in 2017-2019, after the heatwave in the fall of 2015 (Fig. S4), and were complemented with prior surveys conducted in 33 reefs in 2014-2015 reported in Ellis et al. (2019). The two set of surveys, which spanned from 19.1°, to 27.3° N were not performed in the exact same locations but within the same broad geographic regions, so some of the variability in the comparison is due to variability among sites within regions. Surveys were performed at two depths (shallow at  $\leq 5$ m and deep at 5-15m) by SCUBA, although some sites (26 out of 68 total) were surveyed only at one depth (Table S2). During the surveys of 2014-2015, a photo-quadrat belt-transect (196 transects in total) was used along 20 m x 5 m transects, where photos (1 m<sup>2</sup>) were taken every 2 m (see more details in Ellis et al., 2019). During the surveys of 2017-2019, videos were taken along 30 m transects (170 transects in total). To characterize the structure of the benthic community, live coral (scleractinian) and algae (including macroalgae, encrusting, and turf algae) were assessed by extracting 10 still photographs (area of 0.5 and 1 m<sup>2</sup> for the 2014-2015 and 2017-2019 surveys, respectively). Coral Point Count (CPCe; Kohler & Gill, 2006) was used to extract randomly distributed points on each photograph (48 and 20 points extracted from each photograph in 2014-2015 and 2017-2019, respectively). The dominance of algae or coral on the benthos was determined at >50% of absolute algae or coral cover. The proportion of transects that were algae or coral dominated was calculated within regions in the Red Sea.

### Statistical analyses

The best fit for each thermal response curve was determined using nonlinear least squares regression via the  $nlsLM()$  function in the  $minpack.lm$  R package (Padfield et al., 2017).

Bootstrapping methods were then used to estimate the 95% confidence intervals (CI) around the curve and the estimated parameters ( $E$ ,  $E_h$ ,  $T_{opt}$  and  $CT_{max}$ ) and to test differences between

species. We used the bootstrap approach proposed by Thomas, Kremer, Klausmeier, & Litchman (2012) given that the parameters are very sensitive to the number of points past the optimum temperature. A t-test was performed to calculate the differences in  $T_{np=0}$  between groups (coral vs algae).

To calculate the thermal limits of species, a log-logistic response model was fitted using the R package *drc* (Ritz et al., 2015) and  $LT_{50} \pm 95\%$  CI was obtained from the model fit. To assess differences between species in  $LT_{50}$  we compared adjusted 95% CI for simultaneous inferences using the *confint()* function within the *multcomp* R package (Hothorn et al., 2008). Non-overlapping intervals were interpreted as significantly different ( $p < 0.05$ ).

Changes in the benthic community across regions and time (with surveys in 2014-2015 categorized as before the bleaching event and surveys in 2017-2019 as after the bleaching) were assessed using generalized mixed-effects linear models with the *lme()* function from the *nlme* R package (Pinheiro et al., 2015). In the models we included Region (with four levels: Duba, Yanbu-AlWaj, Thuwal and Farasan Banks) and period (with two levels: 2014-2015 and 2017-2019) as categorical predictors. We also add two random factors - depth (with two levels: shallow at  $<5\text{m}$  and deep at  $5\text{-}15\text{m}$ ) and study site (68 in total) – to account for variability within sites and depths. We ran two (independent) models using % live coral and algae cover as dependent variables. To understand changes in the different groups of algae, we perform three additional independent models using % turf algae cover, % encrusting algae cover and % macroalgae cover as dependent variables. Statistical analyses were conducted in R (version 3.6.1) and graphs were created using the *ggplot2* package (Wickham, 2009).

## Results

GPP and NP exhibited a typical unimodal distribution with the performance increasing up to an optimum and then rapidly decreasing with warming as temperature increased (Fig. 1). All species had modest activation energies ( $E$ ) for gross primary (GPP) and net production (NP) in the rising phase of the performance curve (except *T. ornata*), with generally higher thermal dependence ( $E$ ) for algae than coral species (Figs. 1 and 2 and Table 1). On the contrary, deactivation energies ( $E_h$ ) recorded in the falling phase were generally greater for the coral species than the algae, especially for NP (Figs. 1 and 2 and Table 1). The optimum temperature ( $T_{opt}$ ) for both GPP and NP varied greatly among species without clear differences between groups (algae vs corals; Figs. 1 and 2 and Table 1). Similarly,  $CT_{max}$  was greatly variable among

species (Figs. 1 and 2 and Table 1). The temperatures at which algae became net heterotrophic (i.e.,  $T_{np=0}$ ; Fig. 1 and Table 1) were 35.24, 34.38, and 35.74 (for *H. tuna*, *Lithothamnion* sp, and *T. ornata*, respectively) and 32.78 and 33.78 °C for corals (*P. verrucosa*, and *S. pistillata*, respectively). Marginal differences were found between algae and coral for the  $T_{np=0}$  (t-test;  $t = -2.88$ ,  $p = 0.09$ ).

The  $LT_{50}$  (lethal temperature of 50% mortality of individuals) of two of the tropical algae species tested, *H. tuna* and *T. ornata*, were significantly higher than the two species of corals, while for *Lithothamnion* sp. it was not (significance was determined by non-overlapping 95% CI; Table 1 and Fig. 3).

Field surveys showed similar mean live coral cover (mean±SD;  $22.8 \pm 14$  and  $22.3 \pm 18$  % cover) between 2014-2015 and 2017-2019 in the Red Sea (Fig. 4b,c). Coral cover was similar across latitudes in 2014-2015 but not in 2017-2019, as coral cover was lower in the Farasan Banks (the most southern location) than in the other three regions (mean±SD;  $36.5 \pm 14$  % cover in Duba,  $44.5 \pm 16$  in Yanbu-Al Waj,  $26.5 \pm 14$  in Thuwal, and  $13.9 \pm 12$  in the Farasan Banks; Fig. 4b, Table S3). In addition, coral cover decreased from 2014-2015 to 2017-2019 in the Farasan Banks (mean±SD;  $24.94 \pm 16.8$  to  $13.86 \pm 12.2$ , respectively; t-ratio=3.15, p-value=0.042; Fig. 4b and Table S3). Unexpectedly, we found an increase in live coral cover (from  $24.7 \pm 11.81$  to  $44.53 \pm 16.37$  % cover in 2014-2015 and 2017-2019, respectively) in the Yanbu-Al Waj region (t-ratio=-3.19, p-value=0.038; Fig. 4b and Table S3), while in the other two locations, Thuwal and Duba, % live coral cover remained unchanged before and after the bleaching of 2015.

Field surveys also showed similar mean algae cover (mean±SD;  $25.81 \pm 14$  and  $27.21 \pm 19$ ; % algae cover included macroalgae, turf and encrusting algae) in 2014-2015 and in 2017-2019 (Fig. 4c). Across latitudes, algae cover was constant in 2014-2015 but in 2017-2019 it was higher in the Farasan Banks than in the other three more northern locations (mean±SD;  $10.5 \pm 5$  in Duba,  $8.9 \pm 9.9$  in Yanbu-Al Waj,  $15.1 \pm 8.9$  in Thuwal, and  $38.4 \pm 17$  in the Farasan Banks; Fig. 4c, Table S3). Concomitant to the coral cover decrease in the Farasan Banks from 2014-2015 to 2017-2019, the algae cover increased by 55% (from  $24.8 \pm 16.2$  to  $38.4 \pm 17$ ; t-ratio=-3.97, p-value=0.003; Fig. 4b,c and Table S3). Turf algae were the functional group responsible for the increase in algae in the Farasan Banks (Fig. S5 and Table S4). On the other hand, macroalgae and encrusting algae remained rather constant across regions (Fig. S5 and Table S4).

We found that the number of transects with algae cover as the dominant functional group (>50 % benthic cover) increased by over a five fold (from 5 to 26 % of the transects) in the Farasan Banks from 2014-2015 to 2017-2019 (Table S5). In the other three regions (Dubai, Yanbu-Al Waj and Thuwal), there were only a few transects dominated by algae (< 4% of transects) in any of the two sampling periods (Table S5).

## Discussion

Overall, the thermal performance of the focal coral and algae species was variable with the exception of two parameters, the lethal thermal limit ( $LT_{50}$ ) and the deactivation energy ( $E_h$ ). The estimated  $LT_{50}$  of the two coral species (35.7 and 36.1 °C for *P. verrucosa* and *S. pistillata*, respectively) were lower than those estimated for two of the tropical algae species (37.13 and 38 °C for *H. tuna* and *T. ornata*, respectively). This greater thermal tolerance of some algae when compared to coral species suggests a greater resistance to thermal stress. The mean  $LT_{50}$  of the algae *Lithothamnion* sp. (36.3 °C) was close to the coral *S. pistillata* and not significantly different. While red encrusting algae have been suggested to be thermally-resistant in the Caribbean (Anderson, 2006), the Red Sea species tested (*Lithothamnion* sp.) appears to be nearly as sensitive to heat stress as the coral *S. pistillata*. Indeed, red encrusting algae were not observed to increase in abundance southward in the Red Sea (Fig. S5). The lower  $LT_{50}$  of *Lithothamnion* sp. compared to other algae may have consequences for the reef as they provide key ecological roles such as cementing reef fragments into massive structures or providing the settlement cues and substrate for coral larvae (Adey, 1998; Gómez-Lemos et al., 2018; Harrington et al., 2004).

The deactivation energies ( $E_h$ ) achieved in the falling phase revealed high sensitivity to warming once  $T_{opt}$  is surpassed for all species. However, the  $E_h$  of the two coral species were greater than those of *T. ornata* and *Lithothamnion* sp. for GPP and NP. These sharp declines in thermal performance for corals are indicative of their strong thermal-sensitivity once the thermal optimums are exceeded (Table 1), values that are typically surpassed during summer days in shallow reefs in the central Red Sea (Chaidez et al., 2017; Giomi et al., 2019). High  $E_h$  in combination with low  $LT_{50}$  support our hypothesis of a higher vulnerability for coral species during heatwaves, when compared to some of the most common tropical algae species.

The autotrophic capacity of all tested species was suppressed under thermal stress, as indicated by the temperature at which organismal productivity switched from net autotrophic to net heterotrophic ( $T_{np=0}$ ). This temperature ( $T_{np=0}$ ) was nearly 2 °C lower for corals ( $33.28 \pm 0.5$

°C; mean  $\pm$  SE) than for algae ( $35.12 \pm 0.4$  °C; mean  $\pm$  SE). Despite the low replication (n=3 for algae and n=2 for corals) rendering this comparison weak, it may be of biological relevance (Amrhein et al., 2019; Halsey, 2019), as net autotrophic organisms are not viable once their metabolism becomes net heterotrophic. Net productivity in algae is a balance between the metabolic processes of photosynthesis and respiration while for corals involves the complex metabolic coupling between the coral animal, the endosymbiotic algae and the microbial associates (Nelson & Altieri, 2019) – a metabolic balance that is yet insufficiently understood (Hughes et al., 2020). In general,  $T_{np=0}$  can be considered as a proxy for the thermal threshold of organismal viability and we propose  $T_{np=0}$  as a useful metric to compare thermal vulnerability across taxa groups and/or species, as it limits the viability of algae but also compromises that of corals, by leading to a negative oxygen and reduced carbon balance.

Coral bleaching is usually triggered when thermal thresholds are surpassed. These thermal thresholds are often estimated at 1 °C above the long-term maximum monthly mean (MMM) satellite-derived sea surface temperature (SST; Strong, Arzayus, Skirving, & Heron, 2006; Weeks, Anthony, Bakun, Feldman, & Guldborg, 2008), and therefore vary across regions, depending on their local maximum monthly mean SST. Experimental results in the Red Sea, however, do not support this general rule, as four species of corals from Hurghada (northern Red Sea) showed no signs of heat stress (e.g., no coral bleaching observed) after being experimentally exposed to +6 °C (34 °C) relative to their maximum monthly mean of 27.8 °C (Osman et al., 2018). On the other hand, the same coral species from Thuwal (in the central Red Sea) showed significant reductions in physiological performance when exposed to a similar SST, but representing only +3 °C relative to their maximum monthly mean of 31.1 °C (Osman et al., 2018). Additionally, *in situ* mass coral bleaching observations in the Red Sea do not align with recorded thermal anomalies (Cantin et al., 2010; Chaidez et al., 2017; Osman et al., 2018). While coral bleaching is commonly reported after 4 °C degree heat-weeks (DHWs) elsewhere, along with severe coral mortality after 8 °C DHWs (Eakin et al., 2010), in the Red Sea, no bleaching was reported after 15 °C DHWs in several locations. Therefore,  $LT_{50}$  seems to be a better predictor of the upper thermal thresholds for coral species in the Red Sea than DHWs or MMM +1 °C, while also allowing the direct comparison of thermal performance and sensitivity of coral species and algae. However, the estimation of  $LT_{50}$  must be resolved experimentally, which is logistically demanding and has to be done on species individually.

Other thermal parameters (i.e.,  $T_{opt}$  and  $CT_{max}$ ) for GPP and NP varied substantially among species and were not distinctly different across groups (corals vs algae). Although all of the specimens came from the same environment (e.g., a shallow coral reef in the central Red Sea), the large variability in thermal performance among species reflects strong thermal niche differentiation within and across functional groups, arising likely from enhanced resource use efficiency, species evolution and interaction in these diverse communities (García et al., 2018; Loreau & Hector, 2001; Tilman et al., 2001). One of the focal algae species (e.g., *T. ornata*) had an  $E_h$  lower and  $LT_{50}$  higher than both species of corals, which might indicate a greater competitive ability than corals to withstand heat stress. This is surprising, as *T. ornata* is a seasonal species that blooms during the winter-spring months (Prathep et al., 2007); however, small fronds of this macroalgae remain alive in reef crevices and between corals during the summer months (AA personal observation), which could have shaped its wide upper thermal performance curve. The comparative thermal performance of GPP between algae and corals covered all the scenarios that we predicted theoretically (Fig. S1): *Lithothamnion* sp. did not follow any of the predicted scenarios with a  $T_{opt}$  lower than the coral *S. pistillata* and a similar  $LT_{50}$ ; *H. tuna* followed an M2 scenario with similar  $T_{opt}$  and higher  $LT_{50}$  for NP when compared to *S. pistillata*; *T. ornata* followed an M1 scenario (lower  $T_{opt}$  for NP but higher  $T_{lim}$ ) when compared to *S. pistillata*. In summary, while  $T_{opt}$  was species-specific and varied greatly among species, other thermal parameters such as  $LT_{50}$ ,  $E_h$ , and  $T_{np=0}$  clearly indicated lower thermal vulnerability for algae than for coral species.

Our field observations were largely consistent with our empirical findings. We observed a mean decrease in live coral cover (%) in the Farasan Banks (Southern Red Sea) of 44% between surveys in 2014-2015 and in 2017-2019, which is consistent with *in situ* observations of up to 99% of bleached coral colonies in the Farasan Banks in October 2015 at 7° C DHWs (Osman et al., 2018). This loss of almost half of the coral cover aligns with the observations of 40% and 60% coral cover declines reported in the Great Barrier Reef at 4-8° C DHWs after the heatwave of 2016 (Hughes et al., 2018). We did not observe decreases in live coral cover in the other three regions (Duba, Yanbu-Al Waj and Thuwal), of which the Thuwal region in the central Red Sea experienced moderate coral bleaching (between 8-28% of colonies bleached) during the heatwave in 2015 (Monroe et al., 2018; Osman et al., 2018). These results also concur with the findings from the Great Barrier Reef after the 2016 heatwave, where reefs that experienced < 25% bleaching did not undergo noticeable loss of coral cover (Hughes et al., 2018). In fact, coral

cover in the Yanbu- Al Waj region increased by more than 40% between 2014-2015 and 2017-2019. In general, corals in the northern Red Sea are believed to be particularly resistant to warming (Osman et al., 2018), a potential result of floridoside upregulation (an osmolyte and reactive oxygen species scavenger) when exposed to hypersaline conditions prevailing in the northern Red Sea, especially during periods of intense evaporation corresponding to heat anomalies (Gegner et al., 2019; Ochsenkühn et al., 2017).

Concomitant to the coral cover decrease in the Farasan Banks after the bleaching event in 2015, we document an increase of 35% in algae cover from 2014-2015 to 2017-2019. The algal community driving this change in the Farasan Banks was composed of turf filamentous algae (83% of the total algae in 2017-2019). We found that the number of transects of which algae cover was the dominant functional group (>50 % benthic cover and <50 coral cover) increased fivefold from 2014-2015 to 2017-2019 in the Farasan Banks, but not in the other three regions (Duba, Yanbu-Al Waj and Thuwal). This indicates a potential shift in benthic dominance from coral cover to algae following extensive coral bleaching. Contrary to our expectations, we found a very low abundance (mean  $\pm$  SD;  $1.9 \pm 6.59$  % cover) of erect macroalgae (e.g., such as *Turbinaria* sp, *Halimeda* sp. or *Sargassum* sp.) in the Red Sea, including the coral reefs of the Farasan Banks in 2017-2019 (mean  $\pm$  SD;  $0.6 \pm 1.53$  % macroalgae cover). Shallow coral reefs, such those in this study, have been previously identified as environments likely to experience algal proliferation (Graham et al., 2015), presumably due to high light levels that promote algal growth and a greater vulnerability (e.g., mortality) of shallow corals to disturbances such as thermal stress, UV-stress, and storm damage. Our quantitative surveys indicate algal proliferation, mainly of turf algae, in the Farasan Banks following coral bleaching. Turf algae have been suggested to be highly resistant to rising temperatures (Koch et al., 2012), with warming increasing their productivity (Bender et al., 2014). However, we did not experimentally assess the thermal performance and limits of turf benthic algae, which requires further investigation. These algal proliferations in the Farasan Banks could be supported by a combination of factors, such as the higher nutrient availability in the South compared to the northern Red Sea (Kürten et al., 2015; Raitsoos et al., 2013), the moderate and homogenous herbivore pressure long a latitudinal gradient in Saudi Arabia (Kattan et al., 2017; Roberts et al., 2016), and/or subsequent coral mortality due to future heatwaves.

Our experimental results cannot, however, be used as the sole basis for predicting thermal performance of Red Sea reef species, as all experimental assessments involve some degree of oversimplification. The species thermal limits we calculated do not represent an absolute physiological limit, as prolonged exposure to sublethal temperatures may happen during heatwave events, enhancing mortality rates at lower temperatures (Jokiel & Coles, 1977). Furthermore, selection and adaptation may drive algal and coral populations toward resistant forms following future heatwaves.

The thermal optima and  $LT_{50}$  for corals and algae described here are above those for other subtropical and tropical regions (Anderson, 2006; Jokiel & Coles, 1977). This was anticipated, as the Red Sea is the warmest sea in the world, and is heating at twice the global average rate (Chaidez et al., 2017). As such, Red Sea reef species have been shown to be particularly resistant to elevated temperature (Cantin et al., 2010; Osman et al., 2018). Yet, our results show that corals in the Red Sea live near their temperature thresholds, suggesting that future heatwaves, elevated by long-term warming, could have further devastating consequences on corals, particularly in the southern latitudes. The neighboring Arabian Gulf can serve as a grim precedent, as two consecutive thermal anomalies in 1996 and 1998 caused massive coral bleaching and mortality that brought many species to the brink of regional extinction (Riegl et al., 2018) - despite being perceived as particularly resistant to high temperature (Sheppard et al., 1992).

The proliferation of algae on coral reefs have been reported in many reef locations around the world (Graham et al., 2015; Hughes, 1994; Roff et al., 2015). However, observations and experiments demonstrated them to be dependent on elevated nutrient supply or food web effects (Knowlton et al., 1990; McCook et al., 2001), usually involving large coral mortality. We propose here that higher thermal resistance of algae compared to corals, which we determined experimentally, may contribute to explain algal spread following coral bleaching events. Specifically, the thermal resilience of turf algae requires future attention. Future warming of the Red Sea may enhance the likelihood of algal proliferation on reefs by debilitating corals and increasing the competitive ability of certain species of algae. As corals in the southern Red Sea are already growing close to their thermal limit, the prospect of future warming of the Red Sea foretells an increased frequency and severity of heatwaves and, thus, a future prevalence of algae on reefs.

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## Conflict of interest statement

Authors declare no conflict of interest

## Data availability

The data set underlying the study is available at  
<https://doi.pangaea.de/10.1594/PANGAEA.907395>.

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## Tables

**Table 1 | Parameters associated with thermal performance curves for gross primary production (ln GPP) and net production (ln NP+1).** A and C indicate algae and coral, respectively.  $E$  indicates activation energy,  $E_h$  indicates deactivation energy,  $CT_{max}$  indicates the critical thermal limit and  $LT_{50}$  indicates the lethal thermal limit for 50% of the individuals. The unit for  $E$  and  $E_h$  is eV and for the rest of parameters is °C.

Species name	$LT_{50}$ & 95% CI	$T_{opt}$ (GPP) & 95%CI	$E$ (GPP) & 95% CI	$E_h$ (GPP) & 95% CI	$CT_{max}$ (GPP) & 95%CI	$T_{opt}$ (NP&95 %CI)	$E$ (NP)& 95% CI	$E_h$ (NP)& 95% CI	$CT_{max}$ (NP)& 95%CI
<i>Halimeda tuna</i> (A)	37.13 (37.04 – 37.22)	31.68 (0-32.30)	0.57 (0-1.43)	8.24 (6.48 – 11.67)	34.24 (32.88-35.01)	31.97 (31.25-32.58)	0.43 (0.13-0.83)	6.71 (5.06 – 9.81)	35.20 (34.14-35.77)
<i>Lithothamnion sp</i> (A)	36.31 (35.15-36.48)	30.98 (30.84-31.09)	0.69 (0.55 – 0.85)	6.77 (6.55 – 7.05)	33.56 (33.32-33.80)	30.42 (30.32-30.52)	1.60 (1.33 – 1.94)	3.86 (3.75 – 4.01)	31.12 (30.47-31.79)
<i>Turbinaria ornata</i> (A)	38 (37.96 - 38.04)	30.50 (30.03-30.90)	2.09 (1.02-3.65)	6.12 (5.43 – 7.26)	31.36 (30.26-32.53)	29.83 (28.48-30.14)	3.18 (1.53 – 5.70)	4.44 (3.09 – 6.78)	28.19 (27.59-29.82)
<i>Pocillopora verrucosa</i> (C)	35.67 (35.60 – 35.75)	29.87 (28.40-30.33)	0.21 (0.03-0.43)	10.09 (9.80 - 10.40)	32.94 (32.77-33.09)		0 (0-0.21)	12.33 (11.87 – 12.72)	
<i>Stylophora pistillata</i> (C)	36.11 (36.06 - 36.18)	31.91(31.91 -31.91)	0.91 (0.91 – 0.91)	13.70 (13.69 - 13.71)	33.47 (33.47-33.47)	31.36 (31.26-31.45)	0.63 (0.53 – 0.74)	8.75 (8.52 – 8.99)	33.71 (33.57-33.84)

## Figure legends

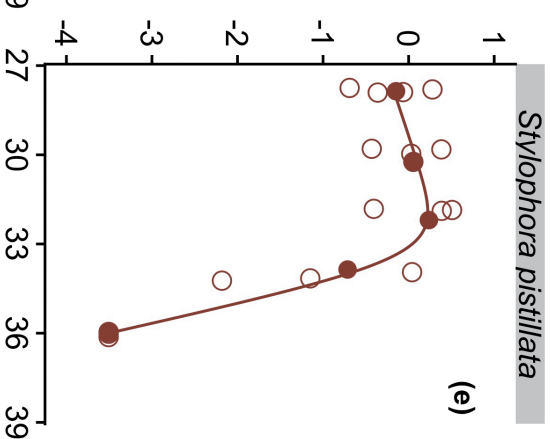
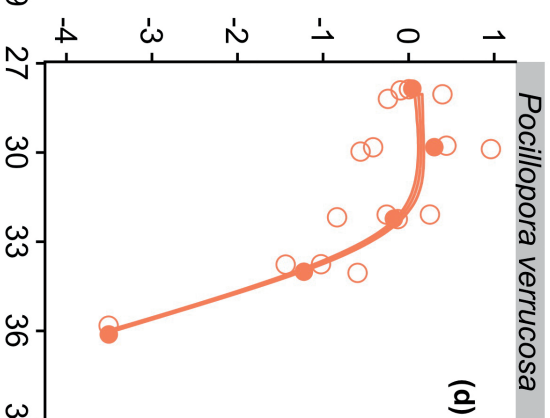
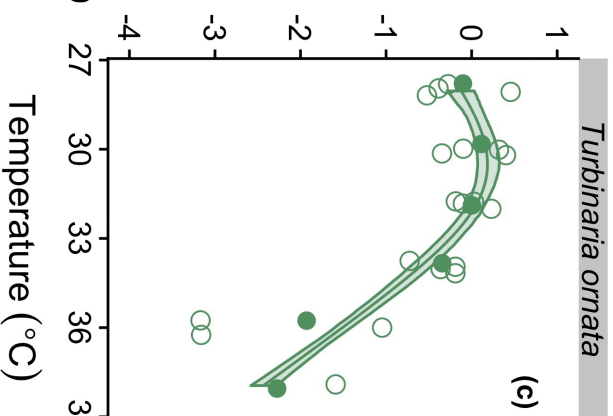
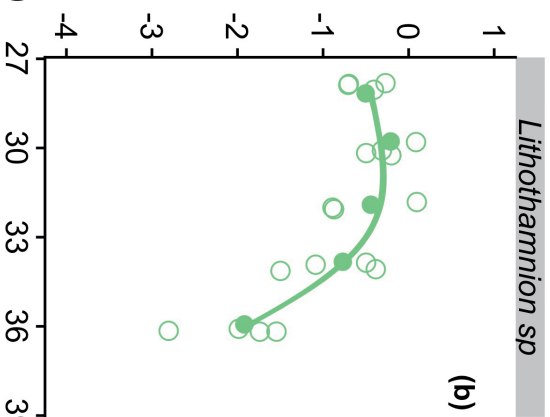
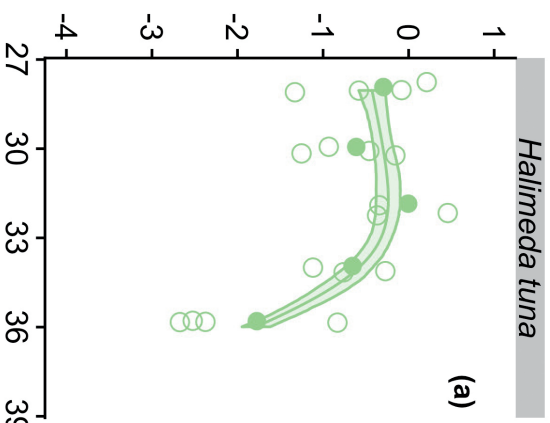
**Figure 1 | Experimental thermal performance curves of gross primary production (GPP, a-e) and net production (NP, f-j) across a temperature gradient from 28 to 38 °C.** Thermal performance curves for the  $\ln$  (GPP) rate and the  $\ln$  (NP+1) rate for the five species of coral and algae presented in shades of red and green, respectively. Empty dots indicate individual measurements and solid dots the mean value for each species at each temperature level. Dashed line in the NP plots indicates NP=0. Illustrations credit: Allende Bodega.

**Figure 2 | Parameters related to thermal performance across a temperature gradient from 28 to 38 °C of the five targeted species for GPP (a-d) and NP (e-h).**  $E$  indicates activation energy,  $E_h$  indicates deactivation energy,  $T_{opt}$  indicates the thermal optimum, and  $CT_{max}$  indicates the critical thermal limit. Coral and algae are presented in shades of red and green respectively. Dots indicate the estimate of the parameter and the error bars range the 95% CI. Different capital letters indicate significant differences at  $p < 0.05$ .

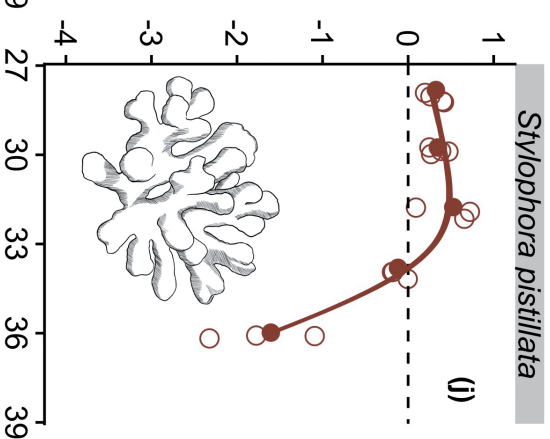
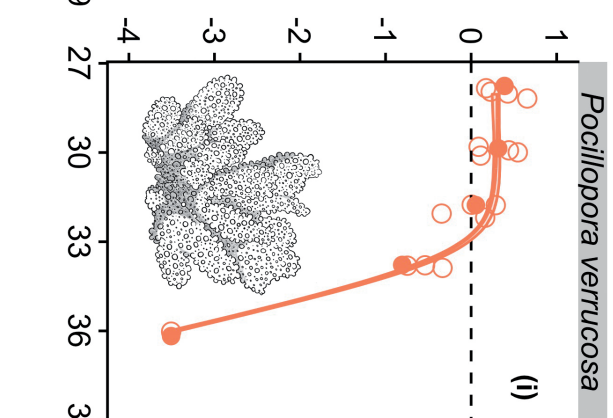
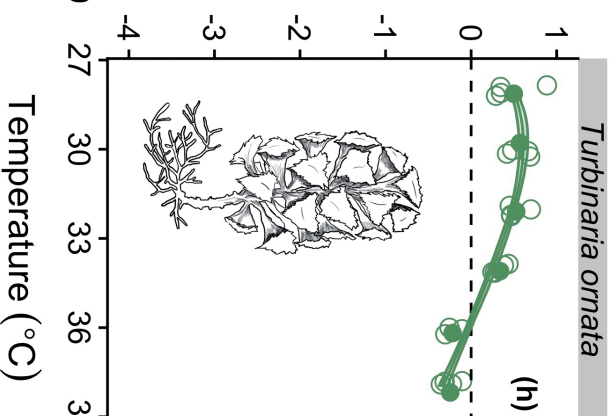
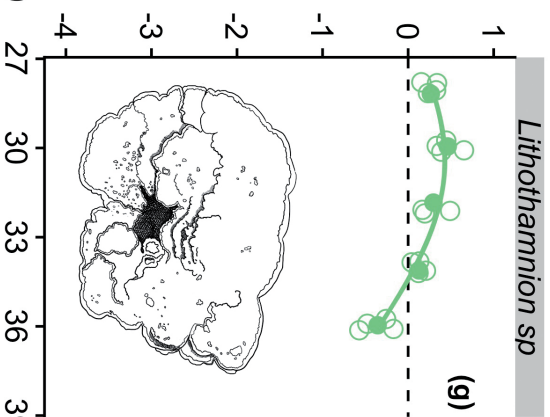
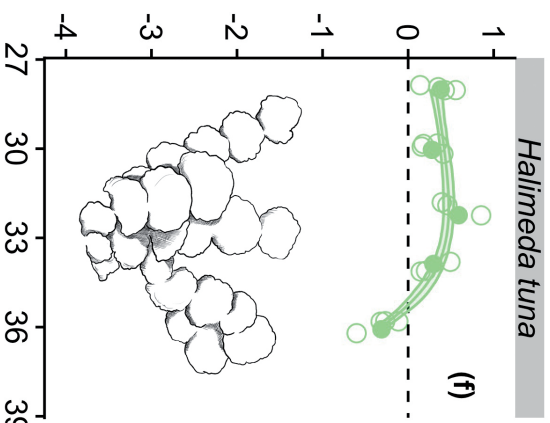
**Figure 3 | Temperature-dependent mortality of the five benthic species along a temperature gradient.** Thermal threshold ( $LT_{50}$ ) reached when 50% of the organisms (indicated with a dashed line) died, with dots indicating the raw measurements, solid lines the fitted model and the grey area the 95%CI (a). Mean and the 95%CI of  $LT_{50}$  (b). Coral and algae are presented in shades of red and green respectively.

**Figure 4 | Live coral and algae cover (%) from video surveys performed in shallow coral reefs (0-15m) before and after the coral bleaching event in 2015 (light triangles and dark circles present surveys in 2014-2015 and 2017-2019, respectively).** Coral bleaching (% of bleached coral colonies in the fall of 2015) was obtained from (Monroe et al., 2018; Osman et al., 2018) and depicted with black circles and triangles respectively (a). Coral (b) and algae (c) are presented in shades of red and green respectively. Open symbols indicate raw data collected at the transect level and solid symbols indicate the mean $\pm$ SE. Algae cover includes erect macroalgae, encrusting algae and turf algae (more information on Table S5).

In GPP ( $\mu\text{mol O}_2 \text{ cm}^{-2} \text{ h}^{-1}$ )



In NP ( $x+1, \mu\text{mol O}_2 \text{ cm}^{-2} \text{ h}^{-1}$ )



Temperature ( $^{\circ}\text{C}$ )

