Title

Worldwide reef surveys highlight different adaptive responses to heat between coral taxa

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Running title

Coral taxa show different heat responses

Abstract

Coral reefs around the world are under threat due to widespread decline of hard corals caused by anomalous heat waves. Different coral taxa are known to have different sensitivities to heat. However, little is known about how long-term effects of heat exposure differ between coral taxa, nor in particular how such effects might drive adaptive processes.

Here, we combined worldwide reef survey data with remotely sensed thermal anomalies to evaluate how local rates of taxa-specific coral cover were associated with heat stress. We found a negative association between coral cover and heat stress, where associations were weaker for massive and encrusting Poritidae, and for meandroid Favidae and Mussidae; and stronger for branching, tabular and cormybose Acroporidae. Additionally, we found that coral cover driven by recent heat stress (measured as the year before a survey) was mitigated by long-term past heat

(measured since 1985) in branching, tabular and cormybose Acroporidae and Pocilloporidae, but not in Poritidae, Favidae and Mussidae. This mitigation of coral decline was not observed under the effect of short-term past heat (measured during the two previous years), suggesting that these presumptive adaptive processes are the result of evolutionary adaptation, rather than of physiological acclimation.

We compared ecological, morphological, physiological and reproductive traits of taxa showing distinct heat-responses, and bring evidence in support of the hypothesis that differential heat-tolerance and growth rates explain the distinct rates of adaptation observed between coral taxa. Further studies should confirm such taxa-specific differences in heat-responses, so that conservation strategies could be adjusted accordingly.

Keywords

Coral reef – coral bleaching – global warming – heat stress – adaptation – remote sensing – life history traits

Main text

Introduction

For more than 30 years now, coral reefs around the world have been suffering from a widespread decline of hard corals (Ateweberhan et al., 2011; De'ath et al., 2012; Cramer et al., 2020). This decline threatens the persistence of the entire coral reef ecosystem, as hard corals constitute the physical architecture of these habitats. A leading cause of this decline is coral bleaching, a stress response driven by heat stress that causes corals to separate from the symbiotic algae living in their tissues (van Oppen and Lough, 2009). When persisting over several weeks, a bleaching state will eventually lead to death of coral (Diaz-Pulido and McCook, 2002). By now, extensive reef deterioration following anomalous heat waves have been observed at a global extent, with a 3.2% absolute loss of coral cover (i.e. the percentage of the reef surface covered by live stony coral) estimated worldwide during the 2005-2015 decade (Souter et al., 2021). By 2050, it is expected that coral bleaching conditions will become persistent worldwide (Van Hooidonk et al., 2013).

The sensitivity to bleaching varies between coral species (Marshall and Baird, 2000; Loya et al., 2001). Over the years, growth form has been considered one of the main proxies to assess bleaching susceptibility, as corals with a branching morphology were observed to be more sensitive to heat stress than corals with an encrusting or a massive morphology (Loya et al., 2001). Coral growth form is correlated with several physiological and metabolic traits, and such correlations were employed to define groups of corals with different life history strategies: such as "stress tolerant", "generalist", "weedy" and "competitive" (Darling et al., 2012). For instance, "stress-tolerant" corals had been defined by a massive morphology with thick corallites (i.e. the skeletal cups containing individual polyps), slow growth rates and high fecundity (Mydlarz et al., 2010; Darling et al., 2012; van Woesik et al., 2012; Conti-Jerpe et al., 2020). However, the assessment of heat-tolerance based on growth forms and life history groups has shown some limitations, since substantial variation in heat-responses can be observed between different species assigned to the same group (Zinke et al., 2018).

Substantial differences in heat tolerance can also be observed between corals from the same species (Bay and Palumbi, 2014; Schoepf et al., 2015). Such tolerance can be the result of adaptive processes driven by previous exposure to thermal stress (Guest et al., 2012; McClanahan, 2017; Hughes et al., 2019). These adaptive processes can occur at two levels: (1) at the physiological level (acclimatization), when a colony temporarily adjusts its metabolism to cope with the stressful condition; and (2) at the genetic level (evolutionary adaptation), when the repeated exposure to stress selects the individuals of a population that carry the genetic traits conferring increased tolerance (Palumbi et al., 2014). Understanding how these adaptive processes contribute to increased heat tolerance in different coral species is of paramount importance in order to organize effective conservation efforts (Matz et al., 2020).

Over the last decade, the combination of field survey records with remote sensed data for sea surface temperature has become one of the main tools used to measure coral decline driven by heat stress. Multiple studies have shown associations between heat stress events and coral cover decline both at local (Head et al., 2019; Babcock et al., 2020; Selmoni et al., 2020a) and global scales (Selig et al., 2012). In other studies, the metric of bleaching intensity was found to be positively associated with heat stress on the Australian Great Barrier Reef (Hughes et al., 2018, 2019), as well as across larger spatial scales (for instance, the Indo-Pacific region; Sully et al., 2019; McClanahan et al., 2020). Notably, some of these studies investigated how past and recent thermal stress interact to drive coral cover decline/bleaching intensity, suggesting the existence of coral adaptation but without being able to distinguish acclimatization from evolutionary

adaptation (Head et al., 2019; Hughes et al., 2019; Sully et al., 2019; Selmoni et al., 2020a). Very few of these works focus on the differences in heat stress responses between coral species (Guest et al., 2012; Hughes et al., 2018; McClanahan et al., 2020), and thus very little information was collected to assess differences in heat stress adaptive potential between coral taxa.

In this study, we combine pre-existing global coral cover data obtained from the Catlin Seaview Survey project (González-Rivero et al., 2014, 2016) with time series of sea surface temperature anomalies computed from remote sensing data by the Coral Reef Watch (Skirving et al., 2020). The goal here is to investigate worldwide how coral decline and adaptation may be driven by heat stress in different coral taxa. We first evaluate how the degree of heat stress experienced by reefs over the past 20 years is associated with local differences in coral cover. These differences concern (1) overall coral cover rates, (2) coral cover rates specific to seven taxa. Next, we assess how such rates of coral cover driven by recent heat stress (measured across the year before the survey) are modulated (i.e. accentuated or mitigated) either by short-term heat stress (measured across the two previous years) or long-term heat stress exposure (measured across more than 20 previous years). We define four groups of coral taxa showing distinct types of heat-responses:

(GR1) negative overall effect of heat stress, modulated by thermal history;

(GR2) negative overall effect of heat stress, without modulation of thermal history;

(GR3) no overall effect of heat stress, but modulation depending on thermal history; and

(GR4) no effect of heat stress, nor modulation of thermal history.

For each of these groups, we referred to the Coral Trait Database (Madin et al., 2016) to highlight ecological, morphological, physiological and reproductive traits that might explain such differences in heat-responses.

Methods

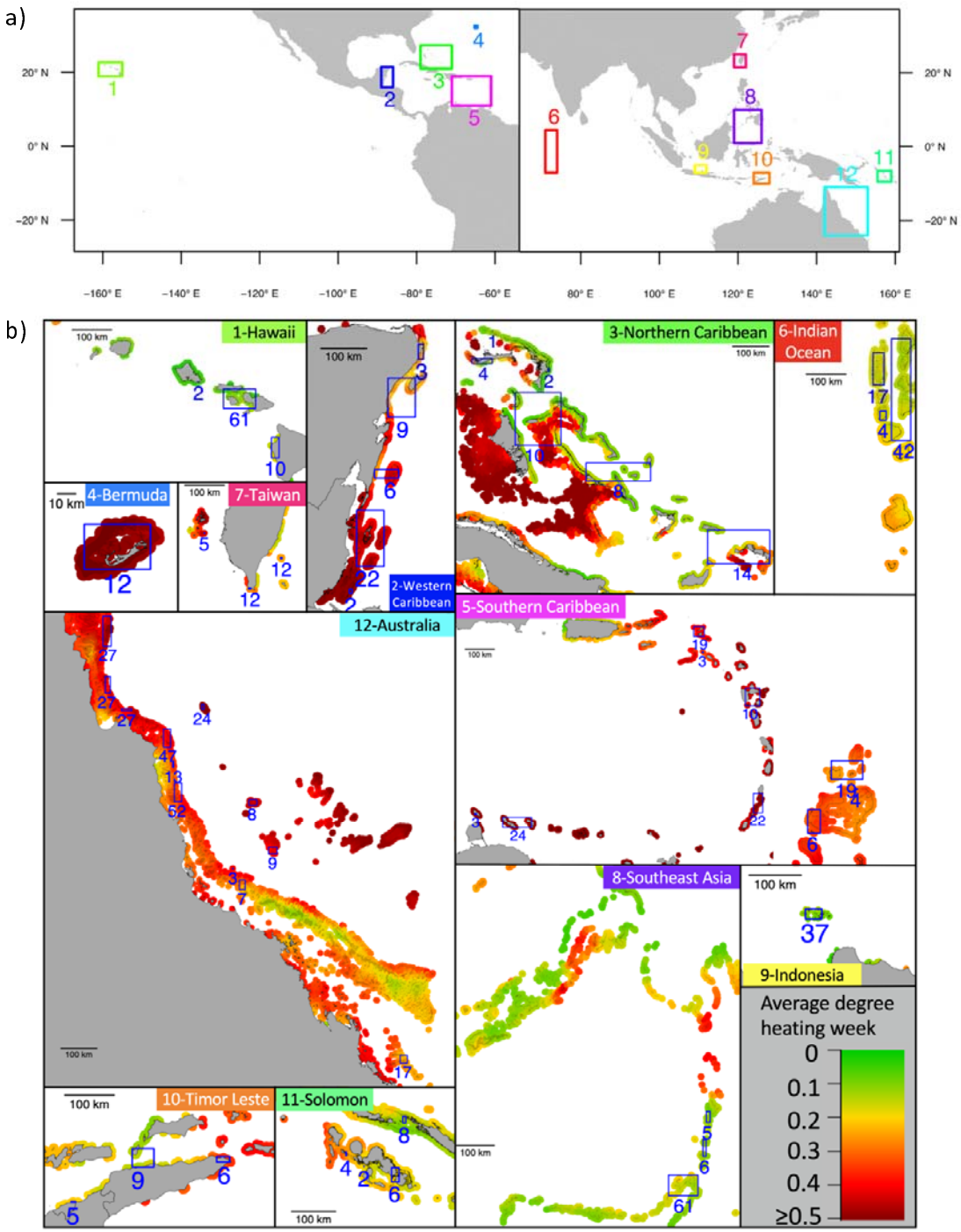
Coral cover data

The coral cover data were obtained from the Catlin Seaview Survey (CSS) project (González-Rivero et al., 2014, 2016). When we accessed the data in January 2021, there were a total of 860 surveys performed along 579 transects (380 transects visited one time, 140 two times, 36 three times, and 23 four times) across twelve study areas around the world between 2012 and 2018 (Fig. 1a). The CSS project applied the same standardized framework to each survey when recording and

analyzing field data. First, field surveys were performed using an underwater 360° camera that took a picture every three seconds along a 1.6-2 km transect, maintaining a constant depth of 10 meters. Next, field pictures were processed using automated image recognition based on machine learning algorithms. Such algorithms were trained using labels that were manually annotated by coral taxonomists (Beijbom et al., 2012).

For each reef survey, the CSS data provided (1) the overall measure of hard coral cover rates and (2) the coral cover rates for 35 taxa of corals labelled using morphological characteristics (e.g. branching Acroporidae, massive Poritidae, meandroid Favidae and Mussidae). We used these data to obtain taxa-specific measurement of coral cover. As the number of labels employed varied between regions, and different regions featured different numbers of surveys, we decided to focus only the labels that appeared in at least half of the twelve study regions. After this filtering, the dataset included taxa-specific coral cover data for the following seven labels: branching Acroporidae (CSS label ACR.BRA), tabular, corymbose, digitate Acroporidae (ACR.TCD), Meandroid Favidae and Mussidae (FAV.MUS), Pocilloporidae (POCI), massive Poritidae (POR.MASS), encrusting Poritidae (POR.ENC), branching Poritidae (POR.BRA).

Figure 1. The study regions. a) Distribution of the twelve study regions. b) For each study region, the map shows the average Degree Heating Week (DHW) values for the 1985-2020 period. The blue squares indicate areas were coral cover surveys from the Catlin Seaview Surveys project were performed, with the numbers corresponding to the number of surveys per area. The reef surfaces were derived from the "Global Distribution of Coral Reefs" dataset of the UNEP (UNEP-WCMC et al., 2021)



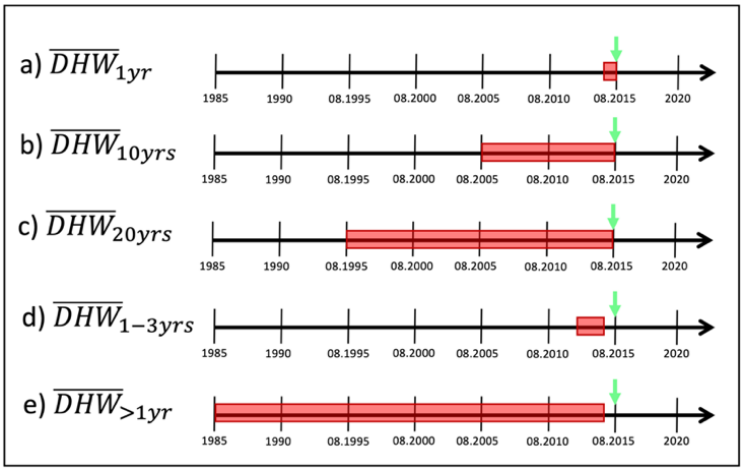
Heat stress data

The heat stress data were retrieved from the Coral Reef Watch database, as part of the 5km-resolution sea surface temperature products (Skirving et al., 2020). The variable we used to

describe heat stress was the Degree Heating Week (DHW, Fig. 1b), as it has been shown to be directly correlated with coral bleaching occurrence and severity (Liu et al., 2014). For a given day, DHW is calculated as the sum of the temperature hotspots (that is, temperatures that exceeded by 1°C the maximal monthly average) from the preceding 12-weeks period. We used the CSS metadata to retrieve the coordinates of every survey location (at the mid-point of the transects), and extracted the daily DHW from 1985 to 2020 for each coordinate using the RASTER R package (v. 3.0; Hijmans, 2016). We discarded 82 surveys for which DHW values could not be extracted due to coordinates located on pixels adjacent to the coastline. In total, we extracted daily DHW values for 778 surveys.

For each reef survey, we computed five different metrics of average DHW (Fig. 2). The first metric represents recent heat stress ( ) and is calculated as the average DHW during the year that preceded the survey date (Fig. 2a). Similarly, we computed an estimation of past heat stress as the average DHW across the 10 years (; Fig. 2b) and the 20 years (; Fig. 2c) that preceded the survey. Additionally, we computed two metrics of past heat stress which excluded the first year before the sampling date. The first of these metrics covers the previous two years (; Fig. 2d), while the second covers all of the previous years (; Fig. 2e). These two variables were developed as estimators of past heat stress that do not overlap with recent heat stress ( ), so that they could be used in bi-variate model construction (see the "Statistical analysis" section).

Figure 2. Degree heating week (DHW) time series averages. The figure displays the differences in the calculation of the five DHW averages used in this study. The green arrows indicate a hypothetical date for the coral cover survey, and the red boxes show the periods of interest for the calculation of average DHW with the different methods.



Statistical analysis

165 Previous studies have employed repeated measures of coral cover over time to determine the
166 trends of coral growth or decline, and then used statistical analyses to match these trends with
167 sea surface temperature data (Selig *et al.*, 2012; Head *et al.*, 2019; Babcock *et al.*, 2020). This
168 approach is not transposable to the CSS dataset, as most of the transects were surveyed only
169 once. For this reason, we employed a different method to investigate how local differences in
170 coral cover rates were associated with historical patterns of heat stress measured at the survey
171 sites.
172 In practice, we investigated the association between coral cover rates and heat stress using
173 generalized linear mixed-models (GLMMs), where the random factors controlled for spatial
174 autocorrelation between survey sites (Dormann et al., 2007). We employed three levels of random
175 factors representing spatial autocorrelation at different spatial scales and progressively nested
176 into each other (*i.e.* the factors covering smaller spatial scales were nested inside those covering
177 larger spatial scales). The first random factor was the study area (twelve levels, Fig. 1a). We then
178 designed two additional random factors to control for spatial autocorrelation at a local scale
179 (within each study area). This was done by applying the following clustering approach in the R
180 environment. First, we computed the Euclidean distances between surveys sites, and applied a
181 hierarchical clustering using the Ward distance method. The result was a tree of distances
182 between survey sites that was used to compute the two additional random factors: (1) survey sites
183 located up to 100 km from each other; and (2) survey sites located up to 7 km from each other.
184 The two threshold values (100 km and 7 km) used in the clustering procedure were chosen as they
185 corresponded to the average value and the minimal value, respectively, of the mean Euclidean
186 distances measured between survey sites within each study area.
187 GLMMs were built using the GLMMTMB R package (v. 1.0; Brooks et al., 2017). We investigated eight
188 response variables recorded at each survey site: overall coral cover and taxa-specific coral cover
189 for seven taxa described in the "Coral cover data" section (ACR.BRA, ACR.TCD, FAV.MUS, POCI,
190 POR.MASS, POR.ENC, POR.BRA). As the coral cover values are percentages between 0 and 1, we
191 used the beta regression method to model their response (Ferrari and Cribari-Neto, 2004). The
192 five explanatory variables were the DHW averages (Fig. 2) described in the "Heat stress data"
193 section: $\overline{DHW}_{1yr}$ (Fig. 2a), $\overline{DHW}_{10yrs}$ (Fig. 2b), $\overline{DHW}_{20yrs}$ (Fig. 2c), $\overline{DHW}_{1-3yrs}$ (Fig. 2d), and
194 $\overline{DHW}_{>1yr}$ (Fig. 2e).
195 We ran the analysis for two types of GLMMs: univariate and bi-variate (Table 1). In univariate
196 GLMMs, we investigated the association of each of the eight response variables with either

$\overline{DHW}_{1yr}$ (M1 in Tab. 1), $\overline{DHW}_{10yrs}$ (M2 in Tab. 1) or $\overline{DHW}_{20yrs}$ (M3 in Tab. 1). The goal was to evaluate how local patterns of coral cover can be explained by recent and past heat stress.

Next, we computed two bi-variate GLMMs for each of the eight response variables. The first bi-variate GLMM investigated the association of the response variable with (1) $\overline{DHW}_{1yr}$ and (2) the interaction between $\overline{DHW}_{1yr}$ and $\overline{DHW}_{1-3yrs}$ (M4 in Tab. 1), while the second model employed (1) $\overline{DHW}_{1yr}$ and (2) the interaction between $\overline{DHW}_{1yr}$ and $\overline{DHW}_{>1yr}$ as explanatory variables (M5 in Tab. 1). The goal of these bi-variate models was to evaluate how past heat stress (measured on the short-term in M4, and on the long-term in M5) modulates (i.e. accentuates or mitigates) the effect of recent heat stress on coral cover.

For each GLMM, we reported the estimate (β, with its standard deviation) and the p-value from the Wald test for the fixed effects. We also computed an approximation of the estimate of the fixed effects (β_{resp}) in the unit scale of the response variable (i.e. in coral cover percentage), using the R-package VISREG (v. 2.7; Breheny & Burchett, 2017) and custom R functions. In addition, we evaluated the goodness-of-fit of each of the GLMMs by measuring the difference between the model's Akaike Information Criterion (AIC; Bozdogan, 1987) and the AIC of a null model. For univariate models, the corresponding null model was a GLMM using a constant value as explanatory variable. For bi-variate models, the null model was the univariate GLMMs using $\overline{DHW}_{1yr}$ as explanatory variable. This approach allowed us to evaluate how accounting for the effect of past heat stress on recent heat stress (i.e. the interaction term of bi-variate models) improves the goodness-of-fit, compared to a model including recent heat stress only ($\overline{DHW}_{1yr}$). According to the rules of thumb for model selection (Burnham and Anderson, 2004), a model with $dAIC < -2$ (where $dAIC = AIC_{null\,model} - AIC_{model}$) has an improved goodness-of-fit, compared to the null model.

Table 1. List of the models computed. The table displays the formulae of the three univariate and two bi-variate models computed for every response variable (CC, representing either overall of taxa-specific coral cover). The explanatory variables used in univariate models are the averages of degree heating weak ($\overline{DHW}$) measured during the year ($\overline{DHW}_{1yr}$), the ten years ($\overline{DHW}_{10yrs}$) and the twenty years ($\overline{DHW}_{20yrs}$) before the survey. In bi-variate models, the explanatory variables are (1) $\overline{DHW}_{1yr}$ and (2) the interaction between $\overline{DHW}_{1yr}$ and $\overline{DHW}$ measured during either the two previous years ($\overline{DHW}_{1-3yrs}$) or all the previous years ($\overline{DHW}_{>1yr}$). α indicates the intercept, β the effects of the explanatory variables.

Univariate models	Bi-variate models
M1) $CC \sim \alpha + \beta(\overline{DHW}_{1yr})$	M4) $CC \sim \alpha + \beta_1(\overline{DHW}_{1yr}) + \beta_2(\overline{DHW}_{1yr} : \overline{DHW}_{1-3yrs})$
M2) $CC \sim \alpha + \beta(\overline{DHW}_{10yrs})$	M5) $CC \sim \alpha + \beta_1(\overline{DHW}_{1yr}) + \beta_2(\overline{DHW}_{1yr} : \overline{DHW}_{>1yr})$
M3) $CC \sim \alpha + \beta(\overline{DHW}_{20yrs})$	

Grouping of taxa based on heat-association

Based on the results of the association study between heat stress and taxa-specific coral cover, we categorized the seven coral taxa retained for the analysis into four groups showing distinct types of heat-associations. The grouping was based on two criteria. First, whether coral cover rates were significantly ($dAIC < -2$) and negatively ($\beta < 0$) associated with recent heat stress ($\overline{DHW}_{1yr}$) in the univariate model M1 (Tab. 1). Second, whether past heat stress ($\overline{DHW}_{>1yr}$) modulated significantly ($dAIC < -2$) the effect of recent heat stress ($\overline{DHW}_{1yr}$) in the bivariate model M5 (Tab. 1). Taxa were assigned to the four heat-association groups as follows:

- Group 1 (GR1): significant decline with recent heat and significant modulation by past heat.
- Group 2 (GR2): significant decline with recent heat, without significant modulation by past heat.
- Group 3 (GR3): non-significant decline with recent heat, significant modulation by past heat.
- Group 4 (GR4): non-significant decline with recent heat and non-significant modulation by past heat.

For every survey, we computed the overall coral cover for every heat-association group as the sum of the taxa-specific coral cover of taxa assigned to every group. Next, we computed the five models of association with heat stress described above (Tab. 1) for the overall coral cover rates of every heat-association group using the same methods described in the "Statistical analysis" section. The goal of these models is to summarize average heat responses for every heat-association group. To visualize such average heat responses we used the VISREG R package (v. 2.7; Breheny & Burchett, 2017) and custom R functions.

Traits of taxa by heat-association groups

We referred to the Coral Trait Database (CTDB; Madin et al., 2016) to compare ecological, morphological, physiological and reproductive traits between coral taxa assigned to the four heat-association groups. The CTDB is a standardized repository storing individual-level (i.e. local records) and species-level (i.e. global estimates) measurements of a wide range of coral traits from published field and experimental studies.

We focused on two individual-level traits: "growth rate" and "water depth"; and three species-level traits: "larval development mode", "sexual system" and "growth form Veron". We chose these traits because they contained large number of measurements, across a large number of taxonomic families worldwide. We downloaded all the CTDB measurements for these traits, and

then proceeded with assigning these measurements to heat-association groups using the following method implemented in a custom R script. First, for every taxon included in a given heat-association group, we retrieved the CSS metadata with the description of the taxon, usually defined by morphology, taxonomical family and region (e.g. Acroporidae with branching morphology in the Indian Ocean). Next, for every taxon, we only retained the CTDB measurements for species matching the corresponding values of morphology, taxonomic family and region. The result was a list of CTDB measurements for the different traits across the four heat-association groups.

We then evaluated the difference in the measurements of such traits between the four heat-association groups. Individual-level measurements, such as those of traits "growth rate" and "water depth", can be prone to bias due to heterogenous sampling (*e.g.* different methods, different regions). To overcome this issue, we decomposed the variance of these traits using random effects models as implemented in the GLMMTMB R package (v. 1.0; Brooks et al., 2017). In these models, we evaluated how the variance of log-transformed "growth rate" and "water depth" were explained by the following random factors: (1) methodology used to perform the measurment; (2) identifier of the study providing the measurement; (3) region and exact location of the measurement; (4) species involved in the measurement; (5) heat-association group of the species involved in the measurement. For the model focusing on "growth rate", we also added a sixth random factor encoding for the water depth at which the measurement was taken. Finally, we computed the estimate effect sizes of the four heat-association groups on the two traits of interest (β_{growth} and β_{depth}), and employed these log-scaled values for a comparison between heat-association groups.

For the three remaining traits, "larval development mode", "sexual system" and "growth form Veron"; measurements corresponded to categorical variables at species-level (e.g. spawner or brooder for "larval development mode", hermaphrodite or gonochore for "sexual system", branching, massive, encrusting or other morphologies for "growth form Veron"). For every trait, we calculated the percentages of the different categories in every heat-association group, and then used these percentages for a comparison between groups.

Results

Univariate models

We first built univariate models to evaluate how coral cover from field surveys was associated with average heat stress ($\overline{DHW}$) calculated over different time periods (1 year, M1; 10 years, M2; and 20 years, M3; Tab. 2a) before the survey dates.

All univariate association models between overall coral cover and past heat stress showed significant ($p < 0.01$) negative ($\beta < 0$) effects and a higher goodness-of-fit than the constant null model ($dAIC < -2$). Such effects were stronger for DHW averages computed over longer periods, with an estimated (absolute) coral cover decline of 3.1 ± 0.3 % for an average of 1°C-week over one year, 11.7 ± 1.7 % over 10 years; and 23 ± 3.9 % over 20 years.

We then focused on taxa-specific rates of coral cover, and observed significant ($p < 0.01; dAIC < -2$) negative ($\beta < 0$) associations with heat stress for all taxa except Pocilloporidae (POCI) and branching Poritidae (POR.BRA). The strongest effects were observed for the two Acroporidae taxa: branching (ACR.BRA) and corymbose, tabular and digitate (ACR.TCD). For ACR.BRA, the estimated decline of coral cover was 0.3 ± 0.1 % for an average of 1°C-week over 1 year, 1.1 ± 0.4 % over 10 years and 2.1 ± 0.6 % over 20 years; and for ACR.TCD these estimates were 0.4 ± 0.1 % over 1 year, 2 ± 0.4 % over 10 years; and 3.7 ± 0.9 % over 20 years.

The other taxa showing a significant negative association were encrusting (POR.ENC) and massive Poritidae (POR.MASS), and meandroid Favidae and Mussidae (FAV.MUS). Compared with the Acroporidae taxa, the estimated coral cover decline was lower and significant only for the heat stress averages covering past 1 and 10 years. The estimated decline of coral cover over 1 and 10 years at average 1°C-week were 0.2 ± 0.1 % and 0.7 ± 0.2 % for POR.ENC, 0.2 ± 0.1 % and 1.1 ± 0.4 % for POR.MASS, 0.3 ± 0.1 % and 1 ± 0.3 % for FAV.MUS, respectively.

Bi-variate models

We employed bi-variate models to evaluate how the associations of coral cover with recent heat stress ($\overline{DHW}_{1yr}$) were modulated by heat stress averages calculated either over the short-term (the previous 2 years, $\overline{DHW}_{1-3yrs}$, M4) or the long-term (all of the previous years since 1985, $\overline{DHW}_{>1yr}$, M5; Tab. 2b).

For short-term heat stress, only the bi-variate model for the taxa POCI showed an increased goodness-of-fit ($dAIC = -2.76$) compared to the null model (*i.e.* the univariate model M1

employing $\overline{DHW}_{1yr}$ as the only explanatory variable). However, the effects of both $\overline{DHW}_{1yr}$ and the interaction term ($\overline{DHW}_{1yr}$: $\overline{DHW}_{1-3yrs}$) in this model did not result as significant ($p > 0.01$). For long-term heat stress, we found bi-variate models with a higher goodness-of-fit than the null model for taxa ACR.BRA, ACR.TCD and POCI. For these three taxa, the effect of recent heat stress ($\overline{DHW}_{1yr}$) on coral cover was of negative sign, whereas the effect of the interaction term (i.e., the modulating effect of long-term heat stress; $\overline{DHW}_{1yr}$: $\overline{DHW}_{>1yr}$) was of positive sign. This indicated that higher levels of long-term heat stress were associated with a mitigation of the negative effect of recent heat stress on taxon-specific coral cover. For instance, for the POCI taxon we estimated 1 year at average 1°C-week to result in a coral cover decline of (1) 0.8 ± 0.1 %, when the long-term average heat stress was below 0.2 °C-week; and of (2) 0.3 ± 0.1 %, when long-term heat stress was above 0.2°C-week. The same comparison for ACR.BRA and ACR.TCD displayed a reduction in coral cover decline from 0.5 ± 0.1 % to 0.4 ± 0.1 % and from 0.9 ± 0.1 % to 0.7 ± 0.1 %, respectively.

Table 2. Coefficients of coral cover – heat association models. The table shows the coefficients describing the three univariate models (a, M1, M2 and M3) and two bi-variate models (b, M4 and M5) associating heat stress ($\overline{DHW}$) with different coral cover variables (one variable per line: overall coral cover - highlighted in grey - and taxa-specific coral cover: ACR.TCD= tabular, corymbose and digitate Acroporidae; ACR.BRA = branching Acroporidae; POR.ENC = encrusting Poritidae; POR.MASS = massive poritidae; FAV.MUS = meandroid Favidae and Mussidae; POCI = Pocilloporidae; POR.BRA = branching Poritidae). $\overline{CC}$ indicates the average coral cover (±standard deviation), $dAIC$ indicates the difference in the Akaike Information Criteria between model and null model (highlighted in bold if $dAIC < -2$, i.e. model has higher goodness-of-fit compared to null model), β shows the estimate effect in beta-regression scale (* if significant effect – p<0.01, red if effect of negative sign, green if positive sign), β_{resp} shows the approximation of the effect in the unit scale of response variable (i.e. in coral cover percentage). In bivariate models (b), β_{resp} of recent heat stress ($\overline{DHW}_{1yr}$) is shown across different levels of short-term past heat stress ($\overline{DHW}_{1-3yrs}$) in M4 and of long-term past heat stress ($\overline{DHW}_{>1yr}$) in M5.

a) Univariate models

		M1) $CC \sim \alpha + \beta(\overline{DHW}_{1yr})$			M2) $CC \sim \alpha + \beta(\overline{DHW}_{10yrs})$			M3) $CC \sim \alpha + \beta(\overline{DHW}_{20yrs})$		
Taxa	$\overline{CC}$	$dAIC$	β	β_{resp}	$dAIC$	β	β_{resp}	$dAIC$	β	β_{resp}
All	17±12%	**-78.46**	-0.22±0.02*	-3.1±0.3%	**-33.46**	-1.05±0.15*	-11.7±1.7%	**-33.46**	-1.84±0.31*	-23±3.9%
ACR.TCD	3±4%	**-24.35**	-0.19±0.04*	-0.4±0.1%	**-14.17**	-1.01±0.23*	-2±0.4%	**-14.17**	-1.83±0.47*	-3.7±0.9%
ACR.BRA	1±3%	**-26.63**	-0.31±0.06*	-0.3±0.1%	**-14.53**	-1.24±0.40*	-1.1±0.4%	**-14.5**	-2.29±0.70*	-2.1±0.6%
POR.ENC	1+2%	**-29.6**	-0.31±0.06*	-0.2±0%	**-2.06**	-0.89±0.31*	-0.7±0.2%	**-2.06**	-1.16±0.62	-0.9±0.5%
POR.MASS	3±4%	**-6.14**	-0.11±0.04*	-0.2±0.1%	**-2.83**	-0.64±0.25*	-1.1±0.4%	**-2.83**	-1.06±0.49	-2±0.9%
FAV.MUS	1±1%	**-11.31**	-0.11±0.03*	-0.3±0.1%	**-4.11**	-0.53±0.17*	-1±0.3%	**-4.11**	-0.82±0.34	-1.7±0.7%
POCI	2±3%	1.82	+0.01±0.03	0±0.1%	0.61	0.21±0.16	0.7±0.6%	0.61	+0.39±0.33	1.4±1.1%
POR.BRA	1±2%	1.86	-0.02±0.06	0±0.1%	1.96	-0.03±0.29	0±0.5%	1.96	+0.11±0.54	0.2±0.9%

b) Bi-variate models

	M4) $CC \sim \alpha + \beta_1(\overline{DHW}_{1yr}) + \beta_2(\overline{DHW}_{1yr}: \overline{DHW}_{1-3yrs})$					M5) $CC \sim \alpha + \beta_1(\overline{DHW}_{1yr}) + \beta_2(\overline{DHW}_{1yr}: \overline{DHW}_{>1yr})$				
Taxa	$dAIC$	β_1	β_2	$\beta_{1_{resp}}$		$dAIC$	β_1	β_2	$\beta_{1_{resp}}$	
				$\overline{DHW}_{1-3yrs} < 0.2$	$\overline{DHW}_{1-3yrs} \geq 0.2$				$\overline{DHW}_{1yr} < 0.2$	$\overline{DHW}_{1yr} \geq 0.2$
All	0.02	-0.24±0.03*	+0.05±0.04	-3.4±0.4%	-3.3±0.4%	-1.67	-0.29±0.04*	+0.30±0.156	-3.9±0.6%	-3.3±0.5%
ACR.TCD	1.69	-0.20±0.05*	+0.03±0.05	-0.5±0.1%	-0.5±0.1%	**-19.37**	-0.69±0.11*	+1.62±0.34*	-0.9±0.1%	-0.7±0.1%
ACR.BRA	1.54	-0.34±0.08*	+0.06±0.09	-0.3±0.1%	-0.3±0.1%	**-5.76**	-0.74±0.17*	+1.52±0.53*	-0.5±0.1%	-0.4±0.1%
POR.ENC	1.98	-0.31±0.08*	+0.01±0.08	-0.2±0.1%	-0.2±0.1%	2	-0.32±0.19	+0.04±0.59	-0.2±0.1%	-0.2±0.1%
POR.MASS	1.8	-0.12±0.04*	+0.03±0.06	-0.2±0.1%	-0.2±0.1%	-1.36	-0.18±0.05*	+0.42±0.22	-0.3±0.1%	-0.2±0.1%
FAV.MUS	1.93	-0.11±0.04*	-0.01±0.04	-0.2±0.1%	-0.2±0.1%	-0.37	0.04±0.11	-0.5±0.33	0.1±0.3%	-0.1±-0.4%
POCI	**-2.76**	-0.04±0.04	+0.08±0.04	-0.1±0.1%	-0.1±0.1%	**-32.86**	-0.39±0.07*	+1.34±0.22*	-0.8±0.1%	-0.3±0.1%
POR.BRA	0.5	-0.09±0.08	+0.10±0.08	-0.1±0.1%	-0.1±0.1%	-0.34	-0.32±0.20	+0.92±0.58	-0.4±0.2%	-0.2±0.1%

330

331 All the coefficients and statistics describing both the univariate and bi-variate association models
332 are displayed in the Supplementary Table 1.

333 *Grouping of taxa by heat-associations*

334

335 Based on the results of the taxon-specific coral cover analysis, we grouped taxa in four groups
336 showing distinct types of heat association.
337 Group 1 (GR1) included ACR.BRA and ACR.TCD, as these are the taxa showing a coral cover decline
338 significantly ($p < 0.01; dAIC < -2$) associated with heat stress ($\overline{DHW}_{1yr}$, $\overline{DHW}_{10yrs}$, $\overline{DHW}_{20yrs}$),
339 and significantly modulated by past long-term heat ($\overline{DHW}_{>1yr}$; M5; Fig. 3a). Indeed, the average
340 models for GR1 showed an estimated coral cover decline of 0.8 ± 0.1 % for an average 1°C-week
341 over 1 year, 3.4 ± 0.7 % over 10 years; and 6.4 ± 1.6 % over 20 years (Fig. 3a, left graph). In GR1,
342 the decline of coral cover associated with recent heat stress ($\overline{DHW}_{1yr}$) appeared to be mitigated
343 by higher levels of long-term heat (Fig. 3a, right graph). For example, one year at average 1°C-
344 week was estimated in a coral cover decline of 1.5 ± 0.2 % if average long-term heat was below
345 0.1°C-week, whereas this decline was reduced down to 0.3 ± 0.1 % when average long-term heat
346 was above 0.4°C-week.
347 Group 2 (GR2) included taxa showing significant heat-associated decline of coral cover, but
348 without significant modulation from past heat stress (Fig. 3b). This group included taxa POR.MASS,
349 POR.ENC and FAV.MUS. The average models for GR2 showed an estimated coral cover decline of
350 0.8 ± 0.2 % for an average 1°C-week over one year, 3.1 ± 0.9 % over 10 years; and 4.7 ± 1.8 %
351 over 20 years (Fig. 3b, left graph). No significant mitigation from past heat was observed for this
352 group, since accounting for the modulating effect of long-term past heat stress
353 ($\overline{DHW}_{1yr}$: $\overline{DHW}_{>1yr}$, M5) did not improve the quality-of-fit ($dAIC > -2$) of the model, compared
354 to the univariate counterpart accounting for recent heat only ($\overline{DHW}_{1yr}$, M1, Fig. 3b, right graph).
355 Group 3 (GR3) included only the POCI taxon. In this group, significant changes of coral cover in
356 association with heat stress could only be detected when considering the modulating role of past
357 long-term heat (Fig. 3c). Indeed, the univariate models (M1, M2, M3) accounting only for past
358 heat stress alone did not improve the quality-of-fit ($dAIC > -2$), compared to a constant null
359 model (Fig. 3c, left graph). However, the bi-variate model (M5) showed significant changes in the
360 association between coral cover and recent heat stress ($\overline{DHW}_{1yr}$), and such changes followed
361 long-term heat stress levels ($\overline{DHW}_{>1yr}$; Fig. 3c, right graph). When long-term heat stress was low,

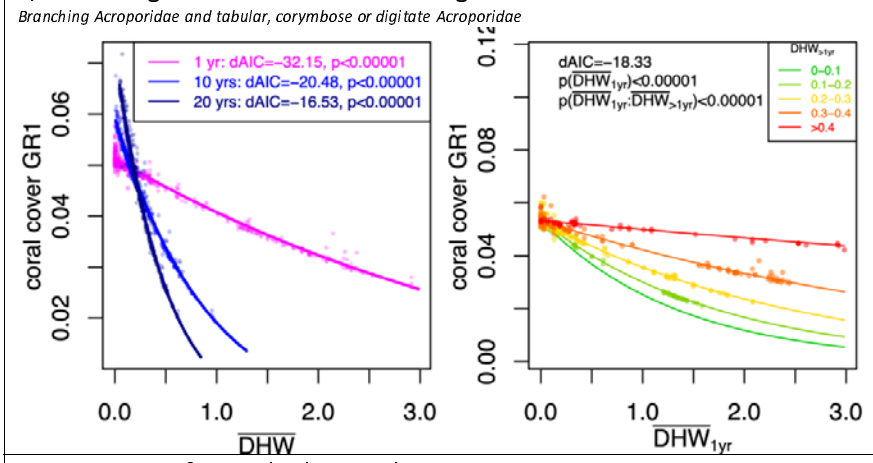
recent heat stress resulted in a negative effect on coral cover, whereas when long-term heat was high, coral cover increased along with recent heat stress. For example, one year at average 1°C-week was estimated in a coral cover decline of if average long-term heat was below 0.1°C-week, whereas coral cover increased of when average long-term heat was above 0.4°C-week.

Group 4 included the only taxa, POR.BRA, for which we couldn't not detect a significant decline of coral cover in association with heat stress, nor a modulating effect associated with long-term past heat stress (Fig. 3d).

Figure 3. Groups of coral cover – heat associations. The plots display the association of coral cover rates with heat stress for four groups of taxa sharing similar heat responses (heat association groups). The graphs on the left display the association of coral cover with average degree heating week ( ) calculated during the year (magenta), the 10 years (blue) and the 20 years (dark blue) that preceded the field survey dates. The graphs on the right side show the association of coral cover with across different ranges of average DHW during all the previous years (i.e. since 1985;). For each association model, the plots display the goodness-of-fit compared to a null model ( ) along with the p-values (p) of the fixed effects. In group 1 (GR1, a), taxa coral cover declines with recent heat, and this decline is mitigated by past heat. In group 2 (GR2, b), taxa coral cover declines with recent heat, without any mitigation by past heat. In group 3 (GR3, c), taxa coral cover doesn't decline with recent heat, but the association between coral-cover and recent heat is modulated by past heat. In group 4 (GR4, d), no significant association between coral cover and heat was found.

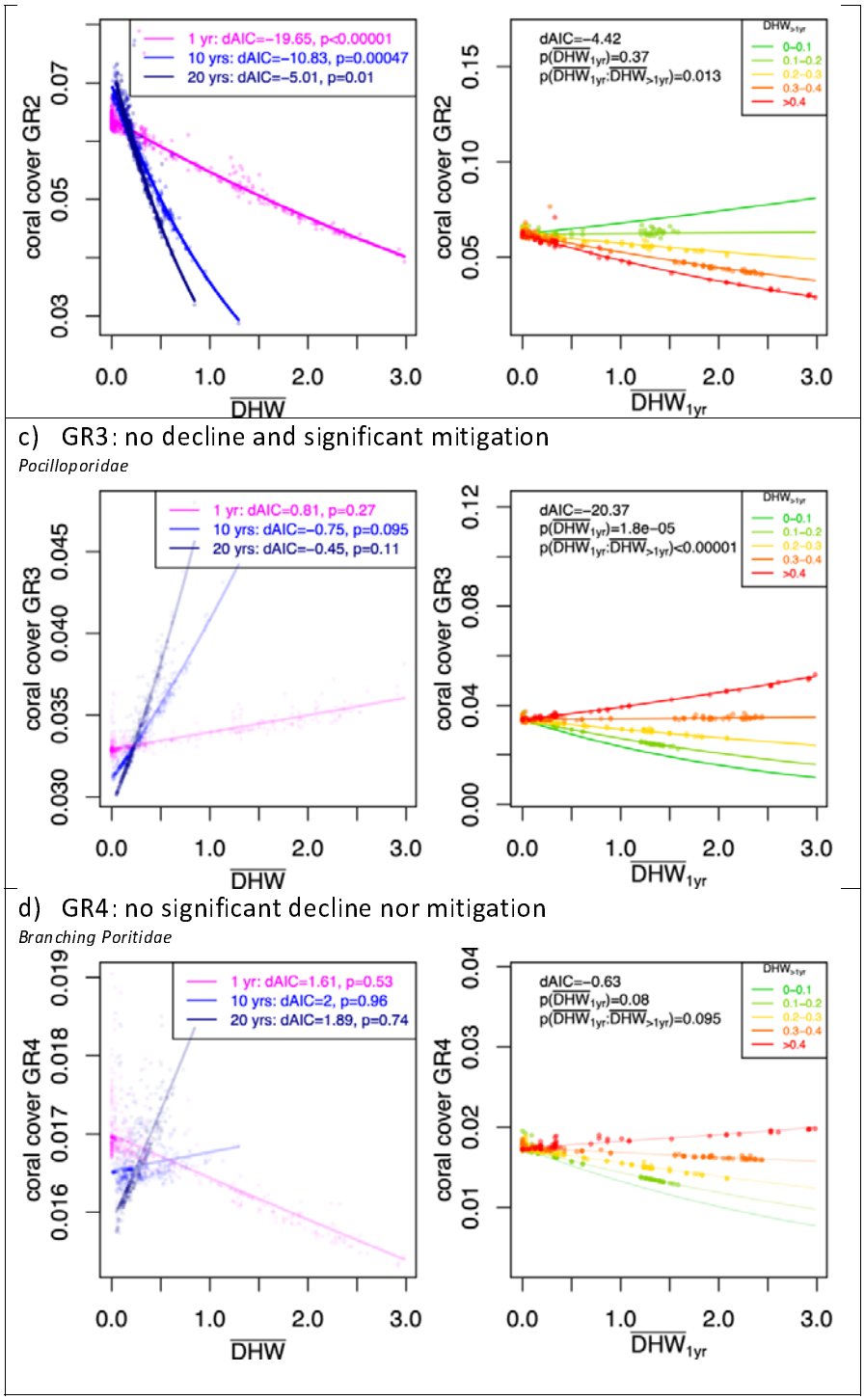
a) GR1: significant decline and mitigation

Branching Acroporidae and tabular, corymbose or digitate Acroporidae



b) GR2: significant decline without mitigation

Massive Poritidae, encrusting Poritidae, Meandroid Favidae and Mussidae



Traits of taxa by heat-association groups

We consulted the Coral Traits Database (CTDB) to evaluate ecological, morphological, physiological and reproductive traits of coral taxa assigned to the four heat-association groups.

375 Corals in GR1 (Tab. 3a) included genera *Acropora*, *Isopora* and *Montipora*. Corals species assigned
376 to GR1 were those displaying the highest growth rates (log-scaled estimate effect $\beta_{growth-GR1} =$
377 $+0.63 \pm 0.31$) and living at the shallowest depth ($\beta_{depth-GR1} = -0.10 \pm 0.09$), in comparison to
378 corals from the other heat-association groups. Coral in GR1 are mostly hermaphrodite (100% of
379 the species in the group) reproducing using a broadcast spawning larval development (94%). The
380 most recurrent growth forms of the species of GR1 are branching (58%), tabular (18%) and
381 corymbose (16%).
382 In GR2 (Tab. 3b), we found corals from genera *Dendrogyra, Goniopora, Isophyllia, Manicina,*
383 *Mycetophyllia, Platygyra* and *Porites*. Compared with corals from the other groups, species from
384 GR2 were estimated with low growth rates ($\beta_{growth-GR2} = -0.40 \pm 0.31$) and to live at shallow
385 depths ($\beta_{depth-GR2} = -0.3 \pm 0.73\, m$). Corals species in GR2 have different larval development
386 modes (71% are spanwers, 29% are brooders) and different sexual systems (40% are
387 hermaphrodite, 60% gonochore). The most recurrent growth forms in GR2 are massive (36%),
388 encrusting (27%) and columnar (12%).
389 GR3 (Tab. 3c) included different genera from the Pocilloporidae family, such as *Stylophora,*
390 *Seriatopora* and *Pocillopora*. The species in this group were estimated with intermediate-high
391 growth rates ($\beta_{growth-GR3} = +0.15 \pm 0.33$) and to live at higher depths ($\beta_{depth-GR3} = +0.21 \pm$
392 0.12), when compared with species from other heat-association groups. Corals species in GR3 are
393 hermaphrodite with different larval development modes (57% of species are spawners, 43%
394 brooders). The most frequent growth forms in GR3 are branching (60%) and encrusting (12%).
395 Coral in GR4 (Tab. 3d) included genera *Goniopora* and *Porites*. Species in this group were
396 estimated to have low growth rates ($\beta_{growth-GR4} = -0.38 \pm 0.42$) and to live at intermediate
397 depth ($\beta_{depth-GR4} = -0.03 \pm 0.11$) when compared with species from other heat-association
398 groups. The reproductive systems of species in GR4 (based on the only two existing trait-
399 annotations for species of the group, *Porites cylindrica* and *Porites compressa*) were spawning and
400 gonochore. The most frequent growth forms in GR4 are branching (54%) and encrusting (26%).

Table 3. Traits of heat-association groups. The table display five traits from the Coral Trait Database for species assigned to the four groups of taxa showing different types of heat-associations. For every group, the first column provides a list of species that are included, β_{growth} represents the log-scaled estimate of the effect of the group on growth rates, β_{depth} represents the log-scale estimate of the effect of the group on water depth, "Larval development" shows the percentage of species in the group using a broadcast spawning or a brooding larval development mode, "Sexual system" shows the percentage of species in the group that are hermaphoridte or gonochore, and "Growth form (Veron)" displays the frequency of the most recurrent morphology types observed among species of the group.

Species ex.	β_{growth}	β_{depth}	Larval development	Sexual system	Growth form (Veron)
a) **GR1: decline and mitigation** *Branching Acroporidae and tabular, corymbose or digitate Acroporidae*					

Acropora aspera, Isopora palifera, Montipora digitata, Acropora millepora, Acropora tenuis, Acropora hyacinthus, Acropora digitifera	+0.63±0.31	-0.10±0.09	Spawner 94% Brooder 6%	100% hermaphrodite	58% branching 18% tables 16% corymbose
b) **GR2: decline without mitigation** *Massive Poritidae, encrusting Poritidae, Meandroid Favidae and Mussidae*					
Porites lutea, Porites lobata, Platygyra sinensis, Porites rus, Goniopora fruticosa, Mycetophyllia ferox, Platygyra lamellina, Isophyllia sinuosa, Dendrogyra cylindrus, Manicina areolata	-0.40±0.31	-0.08±0.10	Spawner 71% Brooder 29%	40% hermaphrodite 60& gonochore	36% massive 27% encrusting 12% columnar
c) **GR3: no decline and mitigation** *Pocilloporidae*					
Stylophora pistillata, Seriatopora hystrix, Pocillopora damicornis, Pocillopora eydouxi, Pocillopora meandrina, Pocillopora verrucosa	+0.15±0.33	+0.21±0.12	Spawner 57% Brooder 43%	100% hermaphrodite	60% branching 12% encrusting 6% columnar
d) **GR4: no decline and no mitigation** *Branching Poritidae*					
Porites cylindrica, Goniopora fruticosa, Porites nigrescens, Porites profundus, Porites monticulosa, Porites compressa, Goniopora palmensis, Porites latistella	-0.38±0.42	-0.03±0.11	Spawner 100%	100% gonochore	54% branching 26% encrusting 7% digitate

Discussion

The global decline of coral cover driven by heat stress

We observed that local rates of coral cover were negatively associated with past heat stress exposure (Fig. 4a). These observations are consistent with previous studies in the field that hypothesized a causal link between heat stress and coral decline (Selig et al., 2012; Hughes et al., 2018; Head et al., 2019; Babcock et al., 2020).

Recent exposure (*i.e.* within one year) to intense heat stress is known to drive a significant decline of coral cover. This was previously shown during the mass coral bleaching event in 2016, which caused a 50% relative decline of coral cover (*i.e.* the ratio of coral cover after and before the event) in the north of the Australian Great Barrier Reef (Hughes et al., 2018) and a 29% decline in the Chagos Archipelago (Indian Ocean; Head et al., 2019). Average DHW values for these two regions in 2016 were ~2.3 and ~3.5°C-week, respectively, and represent heat waves of extreme magnitude. In the present study, recent heat stress was generally below 1°C-week (Fig. 3f), yet even this lower heat stress was significantly associated with coral decline. For instance, one year at an average DHW of 1°C-week was estimated to result in an absolute coral cover decline of ~3% (Fig. 4a).

The recurrence of heat stress events across larger temporal frames (10-20 years) can drive even more severe declines in coral cover. According to our univariate model associating overall coral cover with heat stress averages over ten years ($\overline{DHW}_{10yrs}$, M2), a ten-year average at 1°C-week corresponds to an 11.7% absolute decline of coral cover. As CSS survey locations were exposed to a 0.37°C-week average over the ten years preceding the survey date (Fig. S1), we can estimate

425 that the average 10-years absolute decline of coral cover for all CSS surveys sites was around 4%.
426 This estimate is consistent with the recent report of the Global Coral Reef Monitoring Network,
427 approximating a 3.2% absolute coral cover decline worldwide for the 2005-2015 decade (Souter et
428 al., 2021).
429

430 *Taxon-specific heat responses*

431

432 We classified coral taxa in four groups based on the different types of associations of coral cover
433 with recent and past heat stress. In each of these groups, taxa showed peculiar ecological,
434 morphological, physiological and reproductive traits, some of which might contribute explaining
435 such differences in heat responses.
436 Heat-association group 1 (GR1) was the one showing the highest levels of coral cover decline in
437 response to heat. This result aligns with previous field studies indicating branching, corymbose
438 and tabular *Acropora* and *Montipora* among the most sensitive taxa to heat stress (Loya et al.,
439 2001; Hughes et al., 2018; Pisapia et al., 2019). Our analysis is also consistent with previous local
440 observations reporting increased thermal tolerance in branching Acroporidae after recurrent
441 exposure to thermal stress (Guest et al., 2012; McClanahan, 2017). According to our results, such
442 increased tolerance is more likely to occur through evolutionary adaptation, rather than through
443 acclimation, because long-term heat stress showed a mitigating effect on coral decline, while
444 short-term heat did not. As Guest and colleagues suggested, evolutionary rates in *Acropora* are
445 probably boosted by (1) high sensitivity to heat stress and (2) rapid growth leading to shorter
446 reproductive cycles (Guest et al., 2012). Indeed, our trait characterization showed that corals from
447 GR1 have these physiological and reproductive characteristics. In further support of these
448 hypotheses, recent genotype-environment association studies detected signals of heat adaptation
449 in *Acropora millepora* in the south-western Pacific (Fuller et al., 2020; Selmoni et al., 2021) and
450 *Acropora digitifera* in Japan (Selmoni et al., 2020b). Importantly, in corals from GR1 these
451 presumptive adaptive processes appeared to mitigate the decline driven by recent heat stress, but
452 were not sufficient to neutralize it.
453 Heat-association group 2 (GR2) included massive and encrusting Poritidae, and meandroid Favidae
454 and Mussidae. Corals in GR2 showed a coral cover decline driven by heat stress, even though of
455 lower magnitude when compared to GR1. In contrast, here the thermal history did not appear to
456 modulate the effect of recent heat stress on coral cover. These results were not surprising, as GR2
457 includes corals with of massive morphology that are considered to be stress-tolerant taxa with

458 slow growth, two characteristics that might reduce adaptive rates (Loya et al., 2001; Darling et al.,
459 2012; Guest et al., 2016; Hughes et al., 2018). The absence of a significant adaptive signal in GR2
460 does not necessarily imply that evolutionary adaptation cannot occur in species assigned to this
461 group. In fact, there had been local observations of massive *Porites* populations that acquired
462 thermal resistance from past heat exposure (McClanahan, 2017), as well as reports of other
463 populations that did not (Guest et al., 2012). Either way, our results support the view that the
464 emergence of adaptive responses is less common in massive growth forms from GR2 than in
465 branching growth forms from GR1.
466 Heat association-group 3 (GR3) included corals from the Pocilloporidae family. For corals in this
467 group, we did not observe an overall heat-driven decline of coral cover because the response to
468 recent heat appeared to be strongly related to historical thermal stress. Indeed, when historical
469 heat had been low, corals from GR3 appeared to suffer rates of heat-driven cover decline
470 comparable to corals from GR1; whereas when historical heat had been high, coral cover
471 increased along with recent heat. Local field studies suggested that species from the *Pocillopora*
472 genus might acquire thermal resistance from previous heat exposure (Guest et al., 2012;
473 McClanahan, 2017), and genotype-environment association studies revealed genetic signals of
474 adaptation in *Pocillopora damicornis* and *Pocillopora acuta* (Lundgren et al., 2013; Thomas et al.,
475 2017; Selmoni et al., 2021). However, it is surprising to observe that branching corals from GR3
476 appeared to be more successful in adapting to heat than those from GR1, which have higher
477 growth rates. One possible explanation emerging from our trait analysis is that GR3 includes
478 brooding species (e.g. *Stylophora pistillata*, *Seriatopora hystrix*), whereas in GR1 all species are
479 broadcast spawning. Multiple population genetics studies highlighted that brooding species have
480 more structured populations than broadcast spawning species (Hellberg, 1996; Ayre and Hughes,
481 2000; Selmoni et al., 2021; van der Ven et al., 2021), and this observation likely mirrors the more
482 limited dispersal capabilities of brooding species (Nishikawa et al., 2003). Limited dispersal
483 exacerbates the selective pressure on an adaptive genotype, because individuals carrying this
484 genotype have to persist in the same stressful environment generation after generation (Norberg
485 et al., 2012). Conversely, when dispersal occurs across wider spatial scales, the new recruits can
486 settle and grow in a new region where the thermal constraints driving heat-adaptation are lower
487 or absent, and this might slow down the establishment of an adaptive trait (for instance because
488 of evolutionary trade-offs; Kenkel et al., 2015).
489 Heat-association group 4 (GR4) included branching Poritidae. For this group, we did not observe
490 significant effects of heat stress on coral cover. As mentioned for GR2, the absence of significant

heat-responses does not necessarily imply that heat stress has no effect on these species. Indeed, previous local reports flagged branching *Porites* as "heat-sensitive" (Loya et al., 2001; Guest et al., 2016), and our traits analysis suggests that these species have slower growth rates than those in GR1 and GR3. This might suggest that species from GR4 are unfit for rapid adaptation, an hypothesis that would be consistent with previous work listing branching *Porites* among the "long-term losers" of coral bleaching (van Woesik et al., 2011). Nevertheless, there are also field reports of branching *Porites* acquiring heat-resistance from past thermal exposure (McClanahan, 2017). It is therefore possible that species in GR4 might have very heterogenous heat-responses, and that such responses vary both between different species and between different populations from the same species (McClanahan et al., 2020).

Limitations

In this work, we assumed that local rates of coral cover were driven by the effect of degree heating weeks as measured via remote sensed data. However, coral cover is a general indicator of the state of health of the reef and can be affected by other environmental stressors, many of which are not necessarily related to heat stress (De'ath et al., 2012). This limitation could be mitigated by complementing the association analysis with a wider range of environmental variables that describe other potential stressors for corals survival (such as water pH, turbidity or human pollution). Such analyses could also include additional metrics describing heat stress, in order to determine how the magnitude versus the frequency of thermal anomalies contribute to coral cover decline (McClanahan et al., 2019; Sully et al., 2019).

In this work, we employed taxonomic groups mainly defined by taxonomic family and growth form. In our analysis, we assumed that species belonging to each of these taxa followed similar responses to heat stress. This might not necessarily be the case, as it is possible that within these taxa there are species with divergent heat-responses (for instance, in GR2 and GR4). Furthermore, it is important to underline that the heat-responses that we observed are an average for every taxon, for this average we are not able to evaluate the specific weight of single species. This same issue is likely to affect our trait analysis as well, as the taxonomic composition in the Coral Trait Database is inevitably unbalanced in favor of well-studied species. For instance, the analysis of the reproductive traits of species in GR4 only concerned two species, *P. cylindrica* and *P. compressa*. Future work could focus on re-annotating the CSS surveys with more specific taxonomic labels (for instance, at genus level), so that this analysis could be refined with a higher taxonomic resolution.

Perspectives

The majority of the taxa that we analyzed here showed significant declines in coral cover associated with heat stress. For branching, tabular, corymbose and digitate corals from GR1, evolutionary adaptation might promote coral cover recovery. However, such recovery will likely depend on how widespread the distribution of adapted colonies are presently, and at what rate the adaptive traits would spread across reef systems in the years to come. For massive corals from GR2, the decline appears to be less severe, but the presumptive low rates of evolutionary adaptation raise an alarm: how much additional heat can these taxa tolerate without resorting to evolutionary processes? For Pocilloporidae from GR3, the coral cover decline appeared to be restricted to populations that did not experience thermal stress in the past. For branching Poritidae from GR4, we did not find significant heat responses, but this might be due to highly heterogenous heat responses between different species in this taxon.

The hypotheses formulated in this work should now be tested using field experiments. Genotype-environment association studies have already demonstrated their power for characterizing the potential of evolutionary adaptation in coral populations at local scales (for instance in the central Great Barrier Reef, Fuller et al., 2020; or in New Caledonia, Selmoni et al., 2021). This approach should now be extended to wider spatial scales (for instance the entire south-western Pacific) and consider multiple species with different traits, in order to obtain a more comprehensive view of coral adaptation across reef systems and coral taxa.

Recent studies on coral evolutionary adaptive potential suggest that reef conservation efforts should be oriented toward reefs exposed to recurrent stress, as these might be the sources for adapted corals in the years to come (Matz et al., 2020; Selmoni et al., 2020a). As coral taxa are likely to have different potentials for adaptation (Darling et al., 2012; Guest et al., 2012; McClanahan et al., 2020), the effectiveness of such conservation strategies will also depend on the community structure of the reefs.

Conclusions

We analyzed the association between local rates of coral cover and heat stress at a global scale and found that both recent and past heat stresses are associated with a decline of coral cover. The magnitude of the negative effect of heat stress on coral cover differed between coral taxa, with

lower magnitude in massive and encrusting Poritidae and meandroid Favidae and Mussidae; and higher magnitude in branching, corymbose, tabular and digitate Acroporidae. Furthermore, we found that the negative association between coral cover and recent heat stress appeared to be mitigated by long-term past heat stress in branching Acroporidae and Pocilloporidae. These potential adaptive evolutionary processes were not observed in Poritidae, Favidae and Mussidae. Our analysis is consistent with the hypothesis that heat stress responses mirror distinct physiological and reproductive traits of coral taxa. If confirmed by future studies, this classification of coral taxa by heat-responses would have major implications for coral reef conservation strategies.

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Data Accessibility Statement

Data and code employed in this work are available at https://enacshare.epfl.ch/f8sDnSvGjBMqKFYbyZTEmL7rQVofCNA for review, and will be made publicly available on Zenodo once the article will be accepted for publication.