Title

Worldwide analysis of reef surveys sorts coral taxa by (adaptive) response to heat stress

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Running title

Coral taxa sorted by adaptive 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: weaker for massive and encrusting Poritidae, for meandroid Favidae and Mussidae; and stronger for branching, tabular and corymbose Acroporidae. Additionally, we found that coral cover decline 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 corymbose 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 acclimatization. We finally queried the Coral Trait Database to characterize morphological, physiological and reproductive traits of different taxa showing similar heat-responses. Further genomics studies should confirm the evolutionary origin of such divergent adaptive responses to heat stress.

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). 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 how coral decline and adaptive processes may be driven by heat stress in different coral taxa worldwide. 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 whose distribution spans across different oceans. 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 the 20 previous years). The results sort four groups of coral taxa showing distinct types of heat responses (presence or absence of an overall decline of coral cover) and of adaptive response (presence or absence of a modulating effect of past heat on coral cover decline). For each of these groups, we referred to the Coral Trait Database (Madin et al., 2016) to highlight morphological, physiological and reproductive traits that might explain such differences in heat-responses.

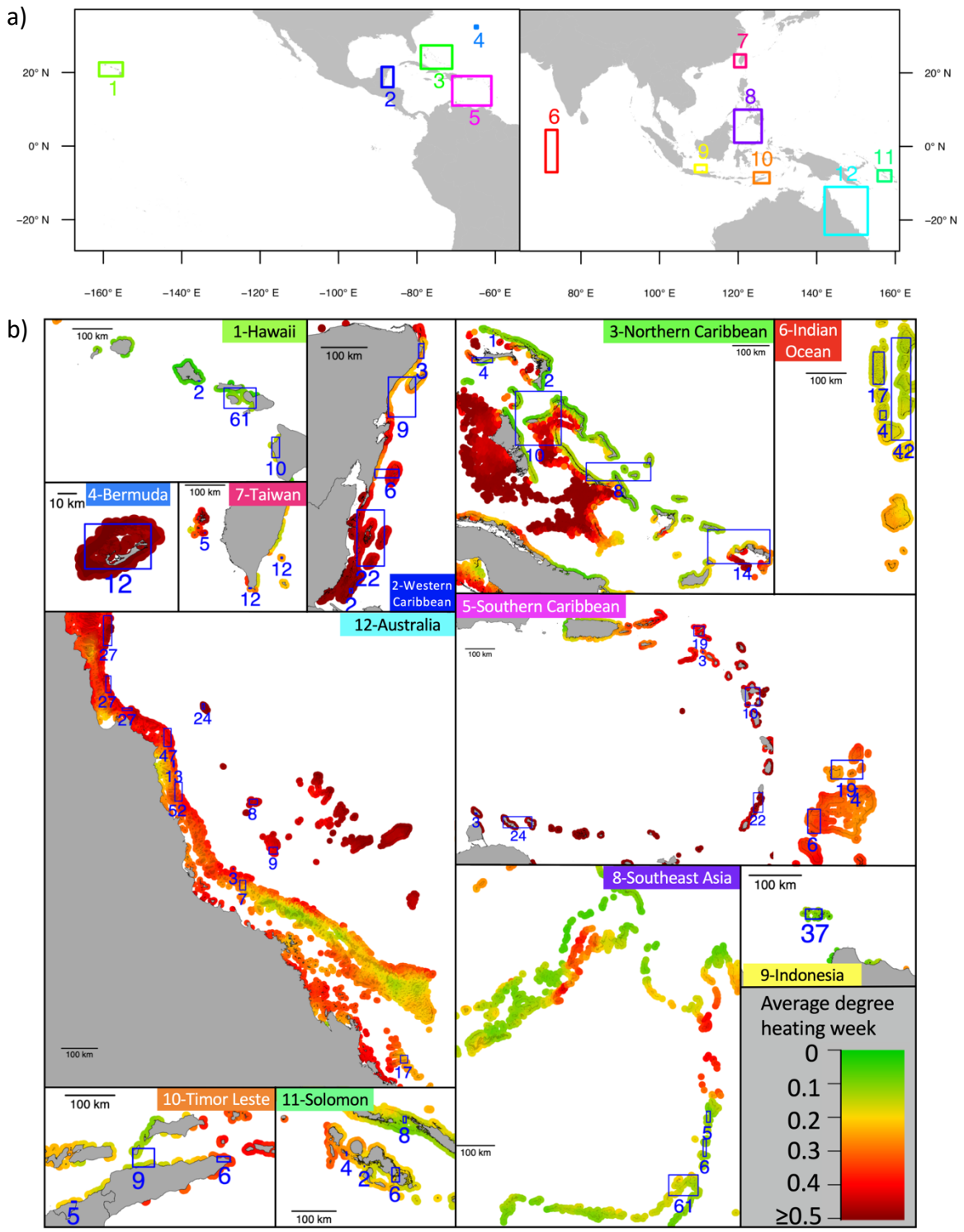
Methods

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 where 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)

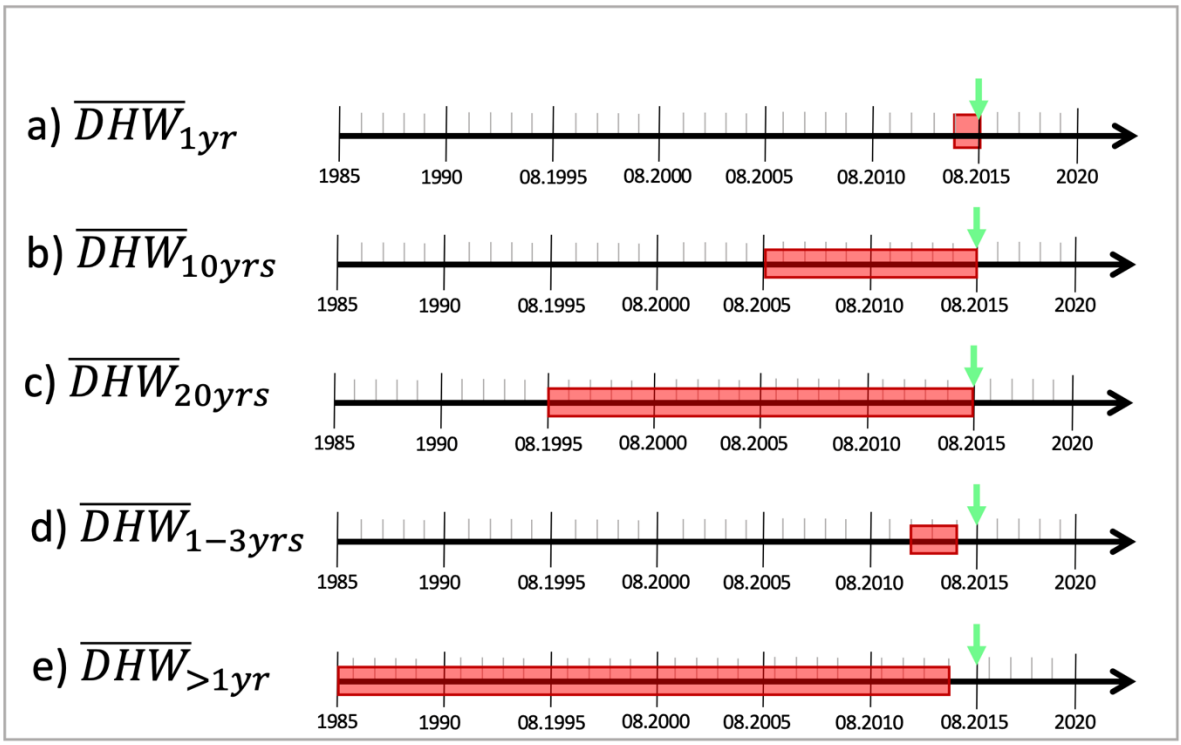


Heat stress data

The heat stress data were retrieved from the Coral Reef Watch database, as part of the 5 km-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 ($\overline{DHW}_{1yr}$) 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 ($\overline{DHW}_{10yrs}$; Fig. 2b) and the 20 years ($\overline{DHW}_{20yrs}$; 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 ($\overline{DHW}_{1-3yrs}$; Fig. 2d), while the second covers all of the previous years ($\overline{DHW}_{>1yr}$; Fig. 2e). These two variables were developed as estimators of past heat stress that do not overlap with recent heat stress ($\overline{DHW}_{1yr}$), 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.



157 *Statistical analysis*

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159 Previous studies have employed repeated measures of coral cover over time to determine the
160 trends of coral growth or decline, and then used statistical analyses to match these trends with sea
161 surface temperature data (Selig et al., 2012; Head et al., 2019; Babcock et al., 2020). This approach
162 is not transposable to the CSS dataset, as most of the transects were surveyed only once. For this
163 reason, we employed a different method to investigate how local differences in coral cover rates
164 were associated with historical patterns of heat stress measured at the survey sites.
165 In practice, we investigated the association between coral cover rates and heat stress using
166 generalized linear mixed-models (GLMMs), where the random factors controlled for spatial
167 autocorrelation between survey sites (Dormann et al., 2007). We employed three levels of random
168 factors representing spatial autocorrelation at different spatial scales and progressively nested into
169 each other (*i.e.* the factors covering smaller spatial scales were nested inside those covering larger
170 spatial scales). The first random factor was the study area (twelve levels, Fig. 1a). We then designed
171 two additional random factors to control for spatial autocorrelation at a local scale (within each
172 study area). This was done by applying the following clustering approach in the R environment. First,
173 we computed the Euclidean distances between surveys sites, and applied a hierarchical clustering
174 using the Ward distance method. The result was a tree of distances between survey sites that was
175 used to compute the two additional random factors: (1) survey sites located up to 100 km from each
176 other; and (2) survey sites located up to 7 km from each other. The two threshold values (100 km
177 and 7 km) used in the clustering procedure were chosen as they corresponded to the average value
178 and the minimal value, respectively, of the mean Euclidean distances measured between survey
179 sites within each study area.
180 GLMMs were built using the GLMMTMB R package (v. 1.0; (Brooks et al., 2017). We investigated eight
181 response variables recorded at each survey site: overall coral cover and taxa-specific coral cover for
182 seven taxa described in the "Coral cover data" section (ACR.BRA, ACR.TCD, FAV.MUS, POCI,
183 POR.MASS, POR.ENC, POR.BRA). As the coral cover values are percentages between 0 and 1, we
184 used the beta regression method to model their response (Ferrari and Cribari-Neto, 2004). The five
185 explanatory variables were the DHW averages (Fig. 2) described in the "Heat stress data" section:
186 $\overline{DHW}_{1yr}$ (Fig. 2a), $\overline{DHW}_{10yrs}$ (Fig. 2b), $\overline{DHW}_{20yrs}$ (Fig. 2c), $\overline{DHW}_{1-3yrs}$ (Fig. 2d), and $\overline{DHW}_{>1yr}$
187 (Fig. 2e).
188 We ran the analysis for two types of GLMMs: univariate and bi-variate (Table 1). In univariate
189 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 and 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 (dAIC; (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) $CC \sim \alpha + \beta(\overline{DHW}_{1yr})$ M2) $CC \sim \alpha + \beta(\overline{DHW}_{10yrs})$ M3) $CC \sim \alpha + \beta(\overline{DHW}_{20yrs})$	M4) $CC \sim \alpha + \beta_1(\overline{DHW}_{1yr}) + \beta_2(\overline{DHW}_{1yr}:\overline{DHW}_{1-3yrs})$ M5) $CC \sim \alpha + \beta_1(\overline{DHW}_{1yr}) + \beta_2(\overline{DHW}_{1yr}:\overline{DHW}_{>1yr})$

214 *Grouping of taxa based on heat-association*

215

216 Based on the results of the association study between heat stress and taxa-specific coral cover, we
217 categorized the seven coral taxa retained for the analysis into four groups showing distinct types of
218 heat-associations. The grouping was based on two criteria. First, whether coral cover rates were
219 significantly ($dAIC < -2$) and negatively ($\beta < 0$) associated with recent heat stress ($\overline{DHW}_{1yr}$) in
220 the univariate model M1 (Tab. 1). Second, whether past heat stress ($\overline{DHW}_{>1yr}$) modulated
221 significantly ($dAIC < -2$) the effect of recent heat stress ($\overline{DHW}_{1yr}$) in the bivariate model M5
222 (Tab. 1). Taxa were assigned to the four heat-association groups as follows:
223 - Group 1 (GR1): significant decline with recent heat and significant modulation by past heat.
224 - Group 2 (GR2): significant decline with recent heat, without significant modulation by past heat.
225 - Group 3 (GR3): non-significant decline with recent heat, significant modulation by past heat.
226 - Group 4 (GR4): non-significant decline with recent heat and non-significant modulation by past
227 heat.
228 For every survey, we computed the overall coral cover for every heat-association group as the sum
229 of the taxa-specific coral cover of taxa assigned to every group. Next, we computed the five models
230 of association with heat stress described above (Tab. 1) for the overall coral cover rates of every
231 heat-association group using the same methods described in the "Statistical analysis" section. The
232 goal of these models is to summarize average heat responses for every heat-association group. To
233 visualize such average heat responses we used the VISREG R package (v. 2.7;(Breheny and Burchett,
234 2017) and custom R functions.

235

236 *Traits of taxa by heat-association groups*

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238 We referred to the Coral Trait Database (CTDB; (Madin et al., 2016) to compare morphological,
239 physiological and reproductive traits between coral taxa assigned to the four heat-association
240 groups. The CTDB is a standardized repository storing individual-level (i.e. local records) and species-
241 level (i.e. global estimates) measurements of a wide range of coral traits from published field and
242 experimental studies.
243 We focused on the "growth rate" individual-level trait and three species-level traits: "larval
244 development mode", "sexual system" and "growth form Veron". We chose these traits because
245 they contained large number of measurements, across a large number of taxonomic families
246 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", 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" was explained by the following random factors: (1) methodology used to perform the measurement; (2) identifier of the study providing the measurement; (3) region and exact location of the measurement; (4) species involved in the measurement; (5) water depth at which the measurement was taken; (6) heat-association group of the species involved in the measurement. Finally, we computed the estimate effect sizes of the four heat-association groups for growth rate (β_{growth}) and employed this log-scaled value 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: $\overline{DHW}_{1yr}$, M1; 10 years: $\overline{DHW}_{10yrs}$, M2; and 20 years: $\overline{DHW}_{20yrs}$, 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 computed 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 computed 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 ($\overline{DHW}_{>1yr}$) 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%

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

Grouping of taxa by heat-associations

Based on the results of the taxon-specific coral cover analysis, we grouped taxa in four groups showing distinct types of heat association.

Group 1 (GR1) included ACR.BRA and ACR.TCD, the taxa showing a coral cover decline significantly ($p < 0.01; dAIC < -2$) associated with heat stress ($\overline{DHW}_{1yr}$, $\overline{DHW}_{10yrs}$, $\overline{DHW}_{20yrs}$), and significantly modulated by past long-term heat ($\overline{DHW}_{>1yr}$; Fig. 3a). Indeed, the average models for GR1 showed an estimated coral cover decline of 0.8 ± 0.1 % for an average 1°C-week computed over 1 year, 3.4 ± 0.7 % over 10 years and 6.4 ± 1.6 % over 20 years (Fig. 3a, left graph). In GR1, the decline of coral cover associated with recent heat stress ($\overline{DHW}_{1yr}$) appeared to be mitigated by higher levels of long-term heat (Fig. 3a, right graph). For example, one year at average 1°C-week was estimated in a coral cover decline of 1.5 ± 0.2 % if average long-term heat ($\overline{DHW}_{>1yr}$) was below 0.1°C-week, whereas this decline was reduced to 0.3 ± 0.1 % when average long-term heat was above 0.4°C-week.

Group 2 (GR2) included taxa showing significant heat-associated decline of coral cover, but without significant modulation from past heat stress (Fig. 3b). This group included taxa POR.MASS, POR.ENC and FAV.MUS. The average models for GR2 showed an estimated coral cover decline of 0.9 ± 0.1 % for an average 1°C-week over one year, 3.2 ± 0.7 % over 10 years; and 5.8 ± 1.5 % over 20 years (Fig. 3b, left graph). No significant mitigation from past heat was observed for this group, since accounting for the modulating effect of long-term past heat stress ($\overline{DHW}_{1yr}$: $\overline{DHW}_{>1yr}$) did not improve the quality-of-fit ($dAIC > -2$) of the model, compared to the univariate counterpart accounting for recent heat only ($\overline{DHW}_{1yr}$, Fig. 3b, right graph).

Group 3 (GR3) included only the POCI taxon. In this group, significant changes of coral cover in association with heat stress could only be detected when considering the modulating role of past long-term heat (Fig. 3c). Indeed, the univariate models (M1, M2, M3 ; Table 1) accounting only for past heat stress alone did not improve the quality-of-fit ($dAIC > -2$), compared to a constant null model (Fig. 3c, left graph). However, the bi-variate model (M5 ; Table 1) showed significant changes in the association between coral cover and recent heat stress ($\overline{DHW}_{1yr}$), and such changes followed

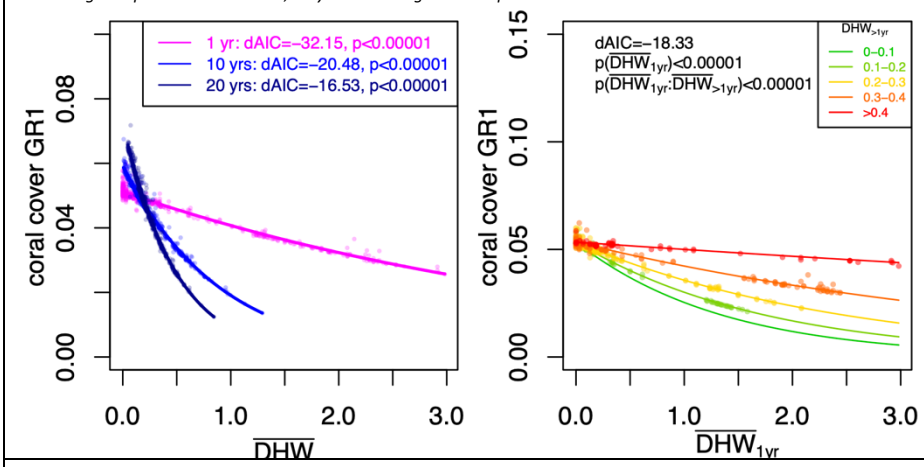
long-term heat stress levels ($\overline{DHW}_{>1yr}$; Fig. 3c, right graph). When long-term heat stress was low, recent heat stress resulted in a negative effect on coral cover, whereas when long-term heat was high, coral cover increased along with recent heat stress. For example, one year at average 1°C-week was estimated in a coral cover decline of 0.8 ± 0.1 % if average long-term heat ($\overline{DHW}_{>1yr}$) was below 0.1°C-week, whereas coral cover increased of 0.6 ± 0.1 % when average long-term heat was above 0.4°C-week.

Group 4 included the only taxa, POR.BRA, for which we could not 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 ($\overline{DHW}$) calculated during the year ($\overline{DHW}_{1yr}$, magenta), the 10 years ($\overline{DHW}_{10yrs}$, blue) and the 20 years ($\overline{DHW}_{20yrs}$, dark blue) that preceded the field survey dates. The graphs on the right side show the association of coral cover with $\overline{DHW}_{1yr}$ across different ranges of average DHW during all the previous years (i.e. since 1985; $\overline{DHW}_{>1yrs}$). For each association model, the plots display the goodness-of-fit compared to a null model ($dAIC$) 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.

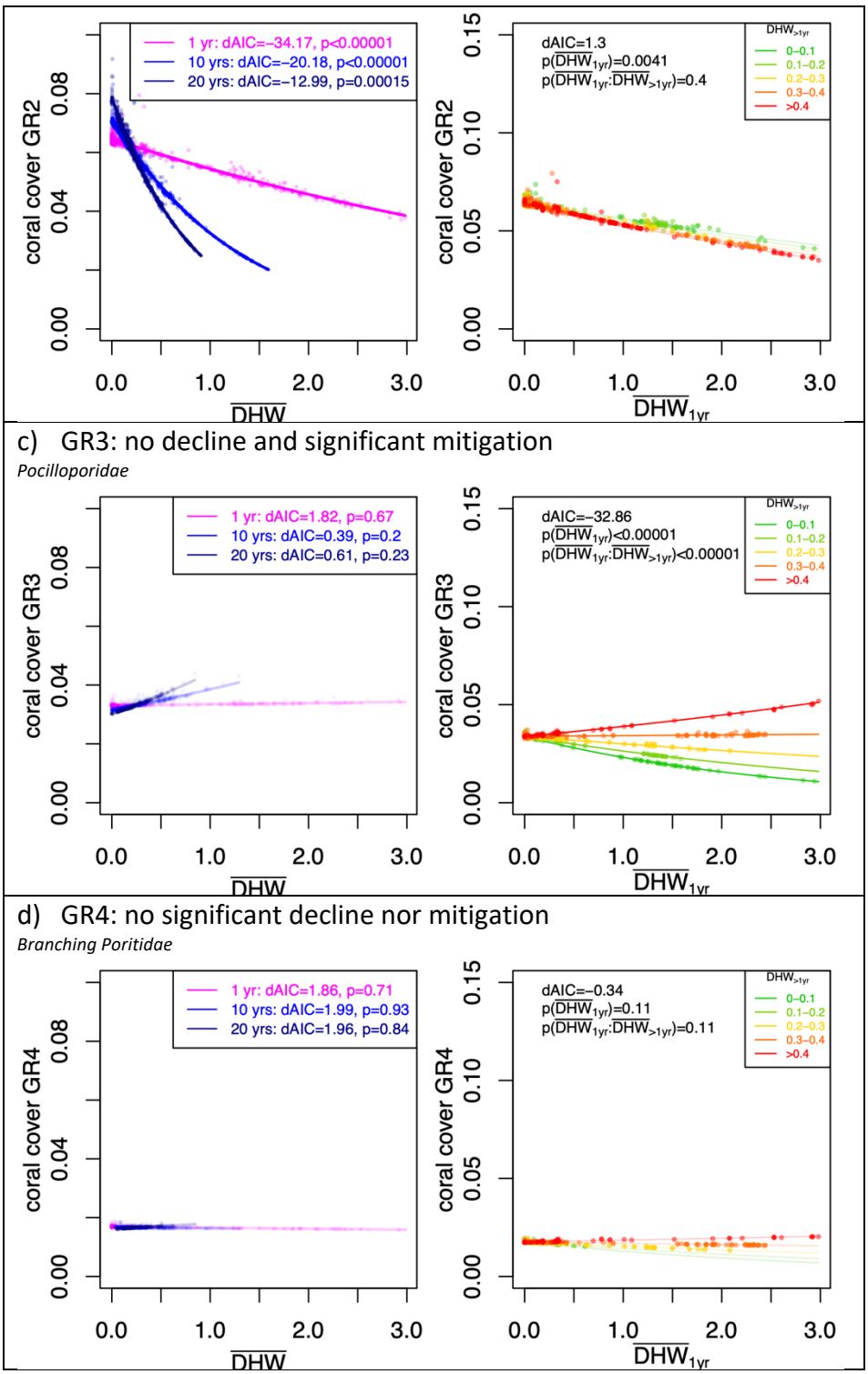
a) GR1: significant decline and mitigation

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 morphological, physiological and reproductive traits of coral taxa assigned to the four heat-association groups.

Corals in GR1 (Tab. 3a) included genera *Acropora*, *Isopora* and *Montipora*. Corals species assigned to GR1 were those displaying the highest growth rates (log-scaled estimate effect $\beta_{growth-GR1} =$

$+0.63 \pm 0.31$), in comparison to corals from the other heat-association groups. Corals in GR1 are mostly hermaphrodite (100% of the species in the group) reproducing using a broadcast spawning larval development (94%). The most recurrent growth forms of the species of GR1 are branching (58%), tabular (18%) and corymbose (16%).

In GR2 (Tab. 3b), we found corals from genera *Dendrogyra, Goniopora, Isophyllia, Manicina, Mycetophyllia, Platygyra* and *Porites*. Compared with corals from the other groups, species from GR2 were estimated with low growth rates ($\beta_{growth-GR2} = -0.40 \pm 0.31$). Corals species in GR2 have different larval development modes (71% are spawners, 29% are brooders) and different sexual systems (40% are hermaphrodite, 60% gonochore). The most recurrent growth forms in GR2 are massive (36%), encrusting (27%) and columnar (12%).

GR3 (Tab. 3c) included different genera from the Pocilloporidae family, such as *Stylophora, Seriatopora* and *Pocillopora*. The species in this group were estimated with intermediate-high growth rates ($\beta_{growth-GR3} = +0.15 \pm 0.33$) when compared with species from other heat-association groups. Corals species in GR3 are hermaphrodite with different larval development modes (57% of species are spawners, 43% brooders). The most frequent growth forms in GR3 are branching (60%) and encrusting (12%).

Coral in GR4 (Tab. 3d) included genera *Goniopora* and *Porites.* Species in this group were estimated to have low growth rates ($\beta_{growth-GR4} = -0.38 \pm 0.42$) when compared with species from other heat-association groups. The reproductive systems of species in GR4 (based on the only two existing trait-annotations for species of the group, *Porites cylindrica* and *Porites compressa*) were spawning and 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, "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}	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	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	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	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	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. 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 (Supplementary Figure S1), 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%.

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 ($\overline{DHW}_{10yrs}$), 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 dates (Supplementary Figure S1), we can estimate that the average 10-years absolute decline of coral cover for all CSS surveys sites was around 4%. This estimate is consistent with the recent report of the Global Coral Reef Monitoring Network, approximating a 3.2% absolute coral cover decline worldwide for the 2005-2015 decade (Souter et al., 2021).

Taxon-specific heat responses

We classified coral taxa in four groups based on the different types of associations of coral cover with recent and past heat stress. In each of these groups, taxa showed peculiar morphological,

419 physiological and reproductive traits, some of which might contribute explaining such differences
420 in heat responses.
421 Heat-association group 1 (GR1) was the one showing the highest levels of coral cover decline in
422 response to heat. This result aligns with previous field studies indicating branching, corymbose and
423 tabular *Acropora* and *Montipora* among the most sensitive taxa to heat stress (Loya et al., 2001;
424 Hughes et al., 2018; Pisapia et al., 2019). Our analysis is also consistent with previous local
425 observations reporting increased thermal tolerance in branching Acroporidae after recurrent
426 exposure to thermal stress (Guest et al., 2012; McClanahan, 2017). According to our results, such
427 increased tolerance is more likely to occur through evolutionary adaptation, rather than through
428 acclimatization, because long-term heat stress showed a mitigating effect on coral decline, while
429 short-term heat did not. As Guest and colleagues suggested, evolutionary rates in *Acropora* are
430 probably boosted by (1) high sensitivity to heat stress and (2) rapid growth leading to shorter
431 reproductive cycles (Guest et al., 2012). Indeed, our trait characterization showed that corals from
432 GR1 have these physiological and reproductive characteristics. In further support of these
433 hypotheses, recent genotype-environment association studies detected signals of heat adaptation
434 in *Acropora millepora* in the south-western Pacific (Fuller et al., 2020; Selmoni et al., 2021) and
435 *Acropora digitifera* in Japan (Selmoni et al., 2020b). Importantly, in corals from GR1 these
436 presumptive adaptive processes appeared to mitigate the decline driven by recent heat stress, but
437 were not sufficient to neutralize it.
438 Heat-association group 2 (GR2) included massive and encrusting Poritidae, and meandroid Favidae
439 and Mussidae. Corals in GR2 showed a coral cover decline driven by heat stress, even though of
440 lower magnitude when compared to GR1. In contrast, here the thermal history did not appear to
441 modulate the effect of recent heat stress on coral cover. These results were not surprising, as GR2
442 includes corals with of massive morphology that are considered to be stress-tolerant taxa with slow
443 growth, two characteristics that might reduce adaptive rates (Loya et al., 2001; Darling et al., 2012;
444 Guest et al., 2016; Hughes et al., 2018). The absence of a significant adaptive signal in GR2 does not
445 necessarily imply that evolutionary adaptation cannot occur in species assigned to this group. In
446 fact, there had been local observations of massive *Porites* populations that acquired thermal
447 resistance from past heat exposure (McClanahan, 2017), as well as reports of other populations that
448 did not (Guest et al., 2012). Either way, our results support the view that the emergence of adaptive
449 responses is less common in massive growth forms from GR2 than in branching growth forms from
450 GR1.

Heat association-group 3 (GR3) included corals from the Pocilloporidae family. For corals in this group, we did not observe an overall heat-driven decline of coral cover because the response to recent heat appeared to be strongly related to historical thermal stress. Indeed, when historical heat was low, corals from GR3 appeared to suffer rates of recent heat-driven cover decline comparable to corals from GR1; whereas when historical heat was high, coral cover increased along with recent heat. Local field studies suggested that species from the *Pocillopora* genus might acquire thermal resistance from previous heat exposure (Guest et al., 2012; McClanahan, 2017), and genotype-environment association studies revealed genetic signals of adaptation in *Pocillopora damicornis* and *Pocillopora acuta* (Lundgren et al., 2013; Thomas et al., 2017; Selmoni et al., 2021). However, it is surprising to observe that branching corals from GR3 appeared to be more successful in adapting to heat than those from GR1, which have higher growth rates. One possible explanation emerging from our trait analysis is that GR3 includes brooding species (e.g. *Stylophora pistillata*, *Seriatopora hystrix*), whereas in GR1 all species are broadcast spawning. Multiple population genetics studies highlighted that brooding species have more structured populations than broadcast spawning species (Hellberg, 1996; Ayre and Hughes, 2000; Selmoni et al., 2021; van der Ven et al., 2021), and this observation likely mirrors the more limited dispersal capabilities of brooding species (Nishikawa et al., 2003). Limited dispersal exacerbates the selective pressure on an adaptive genotype, because individuals carrying this genotype have to persist in the same stressful environment generation after generation (Norberg et al., 2012). Conversely, when dispersal occurs across wider spatial scales, the new recruits can settle and grow in a new region where the thermal constraints driving heat-adaptation are lower or absent, and this might slow down the establishment of an adaptive trait (for instance because of evolutionary trade-offs; Kenkel et al., 2015).

Heat-association group 4 (GR4) included branching Poritidae. For this group, we did not observe 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 cannot adapt rapidly, 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

484 vary both between different species and between different populations from the same species
485 (McClanahan et al., 2020).

486 *Limitations*

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

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

507 *Perspectives*

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

517 significant heat responses, but this might be due to highly heterogenous heat responses between
518 different species in this taxon.
519 The hypotheses supported by this work should now be tested using field experiments. Genotype-
520 environment association studies have already demonstrated their power for characterizing the
521 potential of evolutionary adaptation in coral populations at local scales (for instance in the central
522 Great Barrier Reef, (Fuller et al., 2020); or in New Caledonia, (Selmoni et al., 2021). This approach
523 should now be extended to wider spatial scales (for instance the entire south-western Pacific) and
524 consider multiple species with different traits, in order to obtain a more comprehensive view of
525 coral adaptation across reef systems and coral taxa.
526 Recent studies on coral evolutionary adaptive potential suggest that reef conservation efforts
527 should be oriented toward reefs exposed to recurrent stress, as these might be the sources for
528 adapted corals in the years to come (Matz et al., 2020; Selmoni et al., 2020a). As coral taxa are likely
529 to have different potentials for adaptation (Darling et al., 2012; Guest et al., 2012; McClanahan et
530 al., 2020), the effectiveness of such conservation strategies will also depend on the community
531 structure of the reefs.

532 *Conclusions*

533 We analyzed the association between local rates of coral cover and heat stress at a global scale and
534 found that both recent and past heat stresses are associated with a decline of coral cover. The
535 magnitude of the negative effect of heat stress on coral cover differed between coral taxa, with
536 higher magnitude in branching, corymbose, tabular and digitate Acroporidae; and lower magnitude
537 in massive and encrusting Poritidae and meandroid Favidae and Mussidae. Furthermore, we found
538 that the negative association between coral cover and recent heat stress appeared to be mitigated
539 by long-term past heat stress in branching Acroporidae and Pocilloporidae. These potential adaptive
540 evolutionary processes were not observed in Poritidae, Favidae and Mussidae. Our analysis is
541 consistent with the hypothesis that heat stress responses mirror distinct physiological and
542 reproductive traits of coral taxa. If confirmed by genomic studies, this classification of coral taxa by
543 heat-responses would have major implications for coral reef conservation strategies.
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