

Worldwide analysis of reef surveys sorts coral taxa by associations with recent and past heat stress

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13 Abstract

14 Coral reefs around the world are under threat from anomalous heat waves that are causing the
15 widespread decline of hard corals. Different coral taxa are known to have different sensitivities to
16 heat, although variation in susceptibilities have also been observed within the same species living in
17 different environments. Characterizing such taxa-specific variations is key to enforcing efficient reef
18 conservation strategies.

19 Here, we combine worldwide-reef-survey data with remote sensed environmental variables to
20 evaluate how local differences in taxa-specific coral cover are associated with past trends of thermal
21 anomalies, as well as of non-heat related conditions. While the association with non-heat related
22 environmental variation was seldom significant, we found that heat stress trends matched local
23 differences in coral cover. Coral taxa were sorted based on the different patterns of associations with
24 heat stress.

25 For branching, tabular and corymbose Acroporidae, reefs exposed to recent heat stress (measured the
26 year before the survey) had lower coral cover than locally expected; and among these reefs, those
27 previously exposed to frequent past heat stress (measured since 1985) displayed relatively higher
28 coral cover, compared to those less frequently exposed. For massive and encrusting Poritidae, and for
29 meandroid Favidae and Mussidae, we observed a negative association of coral cover with recent heat
30 stress; however, unlike with Acroporidae, these associations were weaker and did not vary with past
31 heat exposure. For Pocilloporidae, we found a positive association between coral cover and recent
32 heat stress for reefs frequently exposed to past heat, while we found a negative association at reefs
33 less frequently exposed to past heat. A similar pattern was observed for the branching Poritidae,
34 although the associations were weaker and not statistically significant.

35 Overall, these results show taxa-specific heat association patterns that might correspond to taxa-
36 specific responses to past heat exposure, such as shifts in the assembly of coral communities,
37 evolutionary adaptation or physiological acclimation.

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39 1 Introduction

40 For over 30 years now, coral reefs around the world have been suffering from a widespread decline
41 of hard corals (Ateweberhan et al., 2011; De'ath et al., 2012; Cramer et al., 2020). This decline
42 threatens the persistence of entire coral reef ecosystems, as hard corals constitute the physical
43 architecture of such habitats. A leading cause of this decline is coral bleaching, a stress response
44 driven by heat stress that causes corals to separate from the symbiotic algae living in their tissues
45 (van Oppen and Lough, 2009). If this persists over several weeks, a bleaching state will eventually
46 lead to coral death (Diaz-Pulido and McCook, 2002). Extensive reef deterioration following
47 anomalous heat waves have been observed globally, with an estimated 3.2% loss of absolute coral
48 cover (i.e. the percentage of the reef surface covered by live stony coral) worldwide from 2005 to
49 2015 (Souter et al., 2021). By 2050, it is expected that coral bleaching conditions will become
50 persistent worldwide (van Hooidonk et al., 2013).

51 The sensitivity to thermal stress varies between coral species (Marshall and Baird, 2000; Loya et al.,
52 2001; McClanahan et al., 2001). Growth form has typically been considered as one of the main
53 proxies to assess heat stress susceptibility, where corals with branching morphologies were observed
54 to be more sensitive to heat stress than corals with encrusting or massive morphologies (Loya et al.,
55 2001). Coral growth form is correlated with several physiological and metabolic traits (e.g. tissue
56 thickness, fecundity, growth rate), and combination of such traits were employed to define groups of
57 corals with different life history strategies: such as "stress tolerant", "generalist", "weedy" and
58 "competitive" (Darling et al., 2012). As reefs are hit by heat waves, their coral assemblies are shifting
59 toward stress tolerant species (Hughes et al., 2018). Of note, substantial differences in heat tolerance
60 can also be observed between coral of the same species (Bay and Palumbi, 2014; Schoepf et al.,
61 2015; Louis et al., 2016; Klepac and Barshis, 2020; McClanahan et al., 2020b). Such differences can
62 be due to the presence of genetic traits conferring heat tolerance to some colonies of a population
63 (evolutionary adaptation), or to some colonies transiently adjusting their metabolism to cope with a
64 stressful condition (physiological acclimation; Palumbi et al., 2014). Characterizing how responses to
65 past heat exposure (i.e. community shifts, adaptation, acclimation) vary between taxa is of paramount
66 importance in order to organize effective conservation efforts (Baums et al., 2019; Matz et al., 2020).

67 Over the last decade, the combination of field survey records with remote sensed data for sea surface
68 temperature has become one of the major tools used to measure coral decline driven by heat stress.
69 Multiple studies have shown associations between heat stress events and coral cover decline at both
70 local (Head et al., 2019; Babcock et al., 2020; Selmoni et al., 2020a) and global scales (Selig et al.,
71 2012). In other studies, the bleaching intensity metric was found to be positively associated with heat
72 stress on the Australian Great Barrier Reef (Hughes et al., 2018, 2019), as well as across larger
73 spatial scales (for instance, the Indo-Pacific region; Sully et al., 2019; McClanahan et al., 2020a).
74 Notably, some of these studies investigated how past and recent thermal stress interact to drive coral
75 cover decline/bleaching intensity, suggesting the existence of changes in thermal tolerance driven by
76 past heat exposure (Thompson and van Woesik, 2009; Guest et al., 2012; Hughes et al., 2018, 2019;
77 Head et al., 2019; Sully et al., 2019; McClanahan et al., 2020a; Selmoni et al., 2020a). Yet, few of
78 these works focused on the differences in heat stress responses between coral taxa (Guest et al., 2012;

79 Hughes et al., 2018; Head et al., 2019), and even fewer investigated these responses across wide
80 spatial scales (e.g. the entire Indo-Pacific, McClanahan et al., 2020a). Of note, previous studies
81 detected a strong spatial variability in coral heat responses, and suggested that the effects of
82 additional variables (e.g. relating to temperature variability, as well as environmental constraints such
83 as water velocity, sedimentation, eutrophication) might confound or interact with heat stress (Maina
84 et al., 2011; Safaie et al., 2018; McClanahan et al., 2019, 2020a, 2020b; Sully et al., 2022).

85 In the present study, we combine pre-existing global coral cover data obtained from the Catlin
86 Seaview Survey project (González-Rivero et al., 2014, 2016) with time series of sea surface
87 temperature anomalies computed from remote sensed data by the Coral Reef Watch (Skirving et al.,
88 2020). The goal is to investigate how spatial patterns of historical heat stress overlap with local
89 differences in coral cover of different coral taxa. We first evaluate how long-lasting trends of heat
90 stress and alternative environmental constraints (related for instance to water turbidity, salinity and
91 current velocity) are associated with local differences in coral cover. These differences concern (1)
92 overall coral cover, and (2) coral cover specific to seven taxa whose distribution spans across
93 different oceans. Next, we assess how period-specific trends of heat stress associate with local
94 differences in coral cover, and in particular how such associations with recent heat stress (measured
95 across the year before the survey) interacts with (i.e. are accentuated or mitigated by) past heat stress
96 exposure (measured during all the previous years since 1985). The results highlight four groups of
97 coral taxa showing distinct patterns of heat associations.

98 2 Materials and methods

99 2.1 Coral cover data

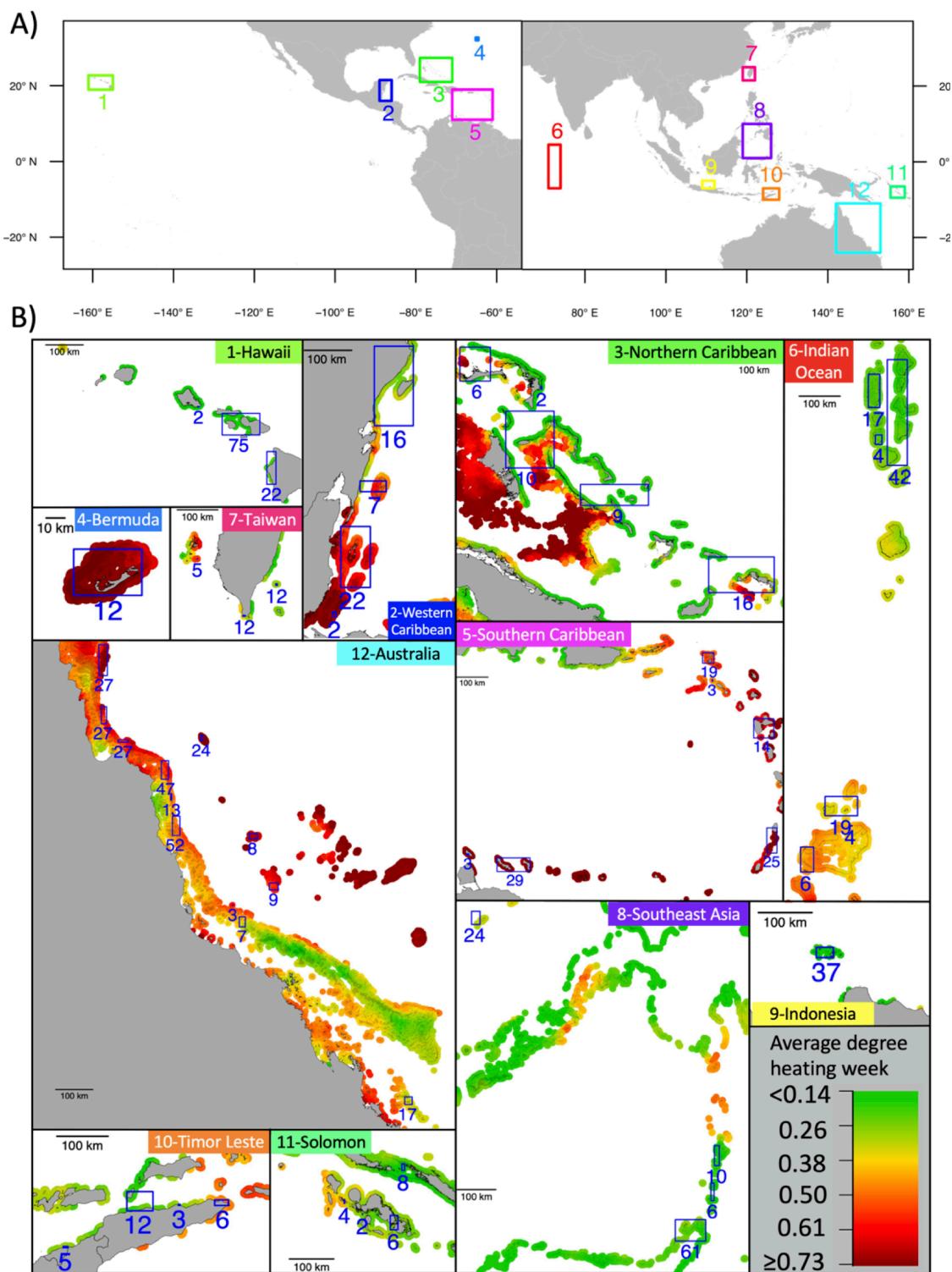
100 The coral cover data were obtained from the Catlin Seaview Survey (CSS) project (González-Rivero
101 et al., 2014, 2016). When we accessed the data in January 2021, there were a total of 860 surveys
102 performed along 579 transects (380 transects were visited once, 140 twice, 36 three times, and 23
103 four times) across twelve study areas around the world between 2012 and 2018 (Figure 1A). The
104 CSS project applied the same standardized framework to each survey when recording and analyzing
105 field data. First, field surveys were performed using an underwater 360° camera that took a picture
106 every three seconds along a 1.6-2 km transect, maintaining a constant depth of 10 meters. Next, field
107 pictures were processed using automated image recognition based on machine learning algorithms.
108 Such algorithms were trained using labels that were manually annotated by coral taxonomists
109 (Beijbom et al., 2012).

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

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Figure 1. The study regions. A) Distribution of the twelve study regions. B) For each study region, the map shows the average monthly maximal 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).



123 **2.2 Environmental data**

124 Environmental data characterizing heat stress data were retrieved from the Coral Reef Watch
125 database, as part of the 5 km-resolution sea surface temperature products (Skirving et al., 2020). The
126 variable we used to describe heat stress was the Degree Heating Week (DHW, Figure 1B), as it has
127 been shown to be directly correlated with coral bleaching occurrence and severity (Liu et al., 2014).
128 For a given day, DHW is calculated as the sum of the temperature hotspots (that is, daily
129 temperatures that exceeded the maximal monthly average by 1°C) from the preceding 12-weeks
130 period. We used the CSS metadata to retrieve the coordinates of every survey location (defined by
131 the transect mid-points) and at each coordinate we extracted the monthly maximal DHW from 1985
132 to 2020 using the RASTER R package (v. 3.0; Hijmans, 2021).

133 Using the same methods, we extracted the monthly averages for different datasets describing
134 seascapes conditions that potentially could be associated with changes in coral cover at survey sites,
135 including:

136 1) chlorophyll concentration (CHL), accessed from the Copernicus Marine Services database
137 (product id: OCEANCOLOUR_GLO_CHL_L4 REP OBSERVATIONS_009_082, spatial
138 resolution: 4 km, temporal window: 1997-2020, EU Copernicus Marine Service, 2017);

139 2) sea current velocity (SCV), accessed from the Copernicus Marine Services database (product id:
140 GLOBAL REANALYSIS PHY_001_030, spatial resolution: ~8 km, temporal window: 1993-2020,
141 EU Copernicus Marine Service, 2017);

142 3) suspended particulate matter (SPM), accessed from the Copernicus Marine Services database
143 (product id: OCEANCOLOUR_GLO_OPTICS_L4 REP OBSERVATIONS_009_081, spatial
144 resolution: 4 km, temporal window: 1997-2020, EU Copernicus Marine Service, 2017);

145 4) sea surface salinity (SSS), accessed from the Copernicus Marine Services database (product id:
146 GLOBAL REANALYSIS PHY_001_030, spatial resolution: ~8 km, temporal window: 1993-2020,
147 EU Copernicus Marine Service, 2017);

148 5) sea surface temperature (SST), accessed from the Coral Reef Watch database (product id:
149 ct5km_sst-mean_v3.1, spatial resolution 5 km, temporal window: 1985-2020; (Skirving et al., 2020).

150 For each of the six datasets (DHW, CHL, SCV, SPM, SSS and SST) used to describe seascapes
151 conditions at the CSS survey locations, we computed three statistics summarizing long-lasting
152 environmental trends: mean (VAR_{MEAN}), standard deviation (VAR_{STD}) and maximal value
153 (VAR_{MAX}). The long-lasting trends covered the entire temporal window from the first measurement
154 of the environmental variable until the date of the CSS survey.

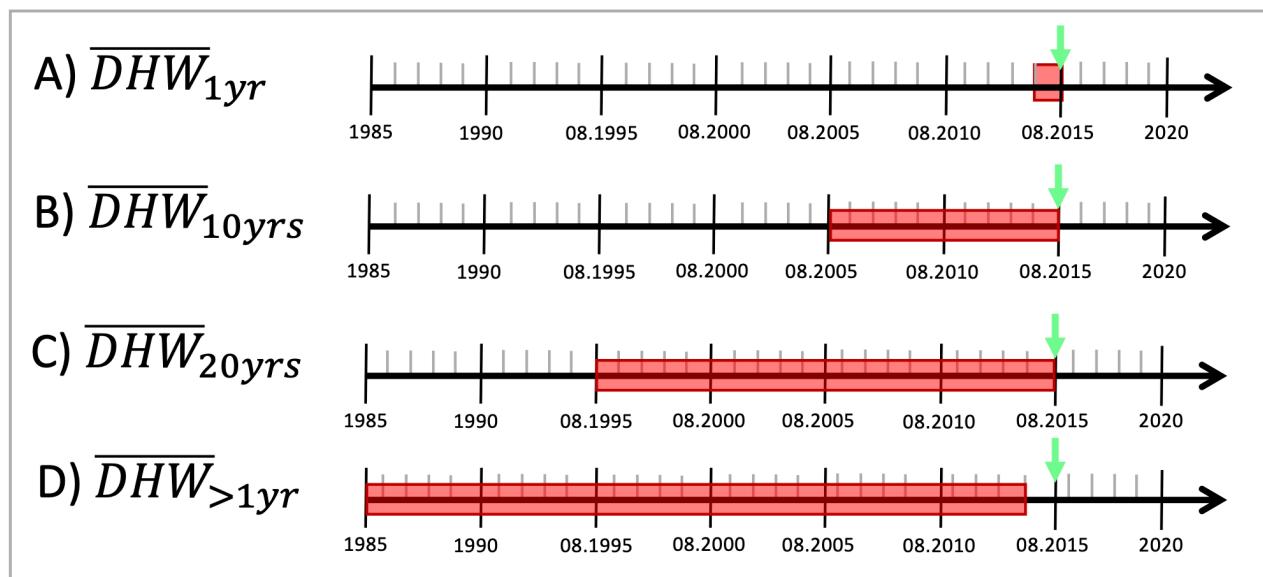
155 For DHW, we computed twelve additional variables that decompose overall trends into period-
156 specific trends of heat stress. These twelve variables were computed using three different statistics:
157 mean ($DHW_{MEAN}_{...}$), standard deviation ($DHW_{STD}_{...}$) and maximal value ($DHW_{MAX}_{...}$), each across
158 four different time periods (Figure 2). The first period represents recent heat stress and covers the
159 year that preceded the survey date ($DHW_{...1yr}$; Figure 2a). Similarly, we defined past heat stress as
160 the periods covering the 10 years ($DHW_{...10yrs}$; Figure 2b) and the 20 years ($DHW_{...20yrs}$; Figure 2c)
161 that preceded the survey. Additionally, we defined one long-term variable of past heat stress which
162 excluded the first year before the sampling date and covered all the previous years ($DHW_{...>1yr}$;

163 Figure 2d). This variable was developed as an estimator of past heat stress that does not overlap with
164 recent heat stress, so that it could be used in bi-variate model construction (see the “Statistical
165 analysis” section).

166 Hereafter, the variable names are abbreviated using the dataset name, followed by the statistics’ name
167 and the time period concerned (i.e., $DHW_{statistics_period}$). For instance, DHW_{STD_10yrs} is the standard
168 deviation of monthly maximum DHW measured across the 120 months (10 years) that preceded the
169 survey date.

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Figure 2. Degree heating week (DHW) periods. The figure summarizes the four temporal windows across which three period-specific DHW statistics (mean, standard deviation, maximal value) were calculated. The timelines are hypothetical examples, where the green arrows indicate a hypothetical date of the coral cover survey, and the red boxes show the periods of interest used to calculate period-specific DHW statistics.



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173 2.3 Statistical analysis

174 Previous studies have employed repeated measures of coral cover over time to determine the trends
175 of coral growth or decline, and then used statistical analyses to match these trends with
176 environmental data (Selig et al., 2012; Head et al., 2019; Babcock et al., 2020). This approach is not
177 transposable to the CSS dataset, as most of the transects were surveyed only once. For this reason, we
178 employed a different method to investigate how local differences in coral cover were associated with
179 patterns of environmental variation measured at the survey sites.

180 In practice, we investigated the association between coral cover and environmental variation using
181 generalized linear mixed-models (GLMMs), where the random factors controlled for spatial
182 autocorrelation between survey sites (Dormann et al., 2007). We employed three levels of random
183 factors representing spatial autocorrelation at different spatial scales and progressively nested into

184 each other (i.e. the factors covering smaller spatial scales were nested inside those covering larger
185 spatial scales). The first random factor was the study area (twelve levels, Figure 1A). We then
186 designed two additional random factors to control for spatial autocorrelation at a regional and at a
187 local scale (within each study area). This was done by applying the following clustering approach in
188 the R environment. First, we computed the Euclidean distances between survey sites, and applied a
189 hierarchical clustering using the Ward distance method. The result was a tree of distances between
190 survey sites that was used to compute the two additional random factors: (1) at regional-level, survey
191 sites located up to 100 km from each other; and (2) at local-level, survey sites located up to 7 km
192 from each other. The two threshold values (100 km and 7 km) used in the clustering procedure were
193 chosen as they corresponded to the average value and the minimal value, respectively, of the mean
194 Euclidean distances measured between survey sites within each study area.

195 GLMMs were built using the GLMMTMB R package (v. 1.0; Brooks et al., 2017). We investigated
196 eight response variables recorded at each survey site: overall coral cover and taxa-specific coral
197 cover for seven taxa described in the “Coral cover data” section (ACR.BRA, ACR.TCD, FAV.MUS,
198 POCI, POR.MASS, POR.ENC, POR.BRA). As coral cover values are percentages, we used the beta
199 regression method to model their response (Ferrari and Cribari-Neto, 2004). For each coral cover
200 variable, we constructed three types of GLMMs (Table 1):

201 **- Univariate GLMMs of long-lasting environmental trends:** the goal of these models is to assess
202 how local patterns of coral cover can be explained by long-lasting trends (mean, standard deviation
203 and maximal value) of variables describing distinct conditions: degree heating week (DHW; M1 to
204 M3 in Table 1A), chlorophyll concentration (CHL: M4 to M6), sea current velocity (SCV: M7 to
205 M9), suspended particulate matter (SPM: M10 to M12), sea surface salinity (SSS: M13 to M15) and
206 sea surface temperature (SST: M16 to M18).

207 **- Univariate GLMMs of period-specific trends of heat stress:** the goal of these univariate models
208 is to evaluate how local patterns of coral cover can be explained by recent and past heat stress. We
209 investigated the association of the coral cover variables with each of the nine explanatory variables
210 describing averages, standard deviations and maximal values of DHW calculated across periods of 1
211 year ($DHW_{...1yr}$; M1 to M3 in Table 1B), 10 years ($DHW_{...10yrs}$; M4 to M6) or 20 years
212 ($DHW_{...20yrs}$; M7 to M9) before the survey.

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Table 1. List of the models computed. The table displays the formulae of the univariate and bi-variate models computed for each coral cover variable (CC, representing either overall or taxa-specific coral cover). Table A) shows the formulae of models for univariate models based on long-lasting environmental trends (mean, standard deviation and maximal value) of degree heating week (DHW; M1-3), chlorophyll concentration (CHL; M4-6), sea current velocity (SCV; M7-9), suspended particulate matter (SPM; M10-12), sea surface salinity (SSS; M13-15) and sea surface temperature (SST; M16-18). Table B) displays the formulae of models based on period-specific trends (mean, standard deviation and maximal value) of DHW measured during the year (M19-21) the ten years (M22-24) and the twenty years (M25-27) before the survey. Table C) shows the formulae of bi-variate models based on the interaction between recent heat stress and past trends of heat stress. The first explanatory variable, representing recent heat stress, is always the maximal value of DHW measured during the year before the survey (DHW_{MAX_1yr}). The second explanatory variable is the interaction of DHW_{MAX_1yr} with the past trends (averages, standard deviations and maximal values) of DHW measured during all of the previous years ($DHW_{...>1yr}$; M28-30). α indicates the intercept, β the effects of the explanatory variables.

A) Univariate models of long-lasting environmental trends		
<i>Degree heating week - DHW</i>	<i>Sea current velocity - SCV</i>	<i>Sea surface salinity - SSS</i>
M1) $CC \sim \alpha + \beta(DHW_{MEAN})$	M7) $CC \sim \alpha + \beta(SCV_{MEAN})$	M13) $CC \sim \alpha + \beta(SSS_{MEAN})$
M2) $CC \sim \alpha + \beta(DHW_{STD})$	M8) $CC \sim \alpha + \beta(SCV_{STD})$	M14) $CC \sim \alpha + \beta(SSS_{STD})$
M3) $CC \sim \alpha + \beta(DHW_{MAX})$	M9) $CC \sim \alpha + \beta(SCV_{MAX})$	M15) $CC \sim \alpha + \beta(SSS_{MAX})$
<i>Chlorophyll concentration - CHL</i>	<i>Suspended particulate matter - SPM</i>	<i>Sea surface temperature - SST</i>
M4) $CC \sim \alpha + \beta(CHL_{MEAN})$	M10) $CC \sim \alpha + \beta(SPM_{MEAN})$	M16) $CC \sim \alpha + \beta(SST_{MEAN})$
M5) $CC \sim \alpha + \beta(CHL_{STD})$	M11) $CC \sim \alpha + \beta(SPM_{STD})$	M17) $CC \sim \alpha + \beta(SST_{STD})$
M6) $CC \sim \alpha + \beta(CHL_{MAX})$	M12) $CC \sim \alpha + \beta(SPM_{MAX})$	M18) $CC \sim \alpha + \beta(SST_{MAX})$
B) Univariate models of period-specific heat stress trends		
<i>1 year period</i>	<i>10 year period</i>	<i>20 year period</i>
M19) $CC \sim \alpha + \beta(DHW_{MEAN_1yr})$	M22) $CC \sim \alpha + \beta(DHW_{MEAN_10yrs})$	M25) $CC \sim \alpha + \beta(DHW_{MEAN_20yrs})$
M20) $CC \sim \alpha + \beta(DHW_{STD_1yr})$	M23) $CC \sim \alpha + \beta(DHW_{STD_10yrs})$	M26) $CC \sim \alpha + \beta(DHW_{STD_20yrs})$
M21) $CC \sim \alpha + \beta(DHW_{MAX_1yr})$	M24) $CC \sim \alpha + \beta(DHW_{MAX_10yrs})$	M27) $CC \sim \alpha + \beta(DHW_{MAX_20yrs})$
C) Bi-variate models of interactions between recent and past heat stress		
M28) $CC \sim \alpha + \beta_1(DHW_{MAX_1yr}) + \beta_2(DHW_{MAX_1yr}: DHW_{MEAN_>1yr})$		
M29) $CC \sim \alpha + \beta_1(DHW_{MAX_1yr}) + \beta_2(DHW_{MAX_1yr}: DHW_{STD_>1yr})$		
M30) $CC \sim \alpha + \beta_1(DHW_{MAX_1yr}) + \beta_2(DHW_{MAX_1yr}: DHW_{MAX_>1yr})$		

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222 **- Bi-variate GLMMs of modulating effects of past heat stress:** the goal of these bi-variate models
 223 is to evaluate how past heat stress interacts (i.e. accentuates or mitigates) with the association
 224 between recent heat stress and coral cover. In practice, the bi-variate models describe the associations
 225 between coral cover variables and two explanatory terms. The first term was the same for all bi-
 226 variate models. This term represents recent heat, and corresponds to the maximal DHW value
 227 measured during the year before the survey (DHW_{MAX_1yr}). We chose this variable as it was the one

228 showing the highest goodness-of-fit for most of the coral cover variables in univariate models (see
229 Results). The second term corresponded to the interaction between (1) DHW_{MAX_1yr} and (2) each of
230 the three explanatory variables describing average, standard deviation and maximum values of DHW
231 calculated over all the previous years ($DHW_{...>1yr}$; M13 to M15). Importantly, the interaction
232 variables describing long-term heat stress trends ($DHW_{...>1yr}$) were weakly collinear with
233 DHW_{MAX_1yr} ($R<0.2$, Supplementary Figure 1).

234 For each GLMM, we reported the estimate (β , with its standard deviation) and the p-value from the
235 Wald test for the fixed effects. We also computed an approximation of the estimate of the fixed
236 effects (β_{resp}) in the unit scale of the response variable (i.e. in coral cover percentage), using the R-
237 package VISREG (v. 2.7; Breheny and Burchett, 2017) and custom R functions.

238 In addition, we evaluated the goodness-of-fit of each of the GLMMs by measuring the difference
239 between the model's Akaike Information Criterion ($dAIC$; Bozdogan, 1987) and the AIC of a null
240 model. For univariate models, the corresponding null model was a GLMM using a constant value as
241 explanatory variable. For bi-variate models, the null model was the univariate GLMMs using
242 DHW_{1yr} as explanatory variable (M21). This approach allowed us to evaluate how accounting for the
243 interaction with past heat stress improves the goodness-of-fit, compared to a model including recent
244 heat stress only (DHW_{1yr}). According to the rules of thumb for model selection (Burnham and
245 Anderson, 2004), a model with $dAIC < -2$ (where $dAIC = AIC_{null\ model} - AIC_{model}$) has an
246 improved goodness-of-fit, compared to the null model.

247 For each GLMM, we calculated the coefficients of variation (CV) related to the three random factors
248 accounting for spatial autocorrelation (at study area-, regional- and local-level). CV was calculated
249 by dividing the conditional standard deviation of every random factor by the intercept value of the
250 model. In practice, these CVs could then be used as scaled standard deviations to compare the
251 amount of variance controlled by every random factor across the different models (higher CV
252 indicates larger amount of variance).

253 2.4 Grouping of taxa based on heat association

254 Based on the results of the association study between heat stress and taxa-specific coral cover, we
255 categorized the seven coral taxa retained for the analysis into four groups showing distinct types of
256 heat associations. The grouping was based on two criteria. First, whether differences in coral cover
257 were significantly ($dAIC < -2$) associated with recent heat stress (DHW_{MAX_1yr}) in the univariate
258 model M21 (Table 1B). Second, whether past heat stress ($DHW_{MEAN_>1yr}$) interacted significantly
259 ($dAIC < -2$) with recent heat stress (DHW_{MAX_1yr}) in the bivariate model M28 (Table 1C). We
260 chose M21 and M28 as these models display the highest goodness-of-fit in the association models
261 with the majority of the coral cover variables (see Results). Taxa were assigned to the four heat
262 association groups as follows:

- 263 - Group 1 (GR1): significant association of local coral cover with recent heat, significant interaction
264 with past heat.
- 265 - Group 2 (GR2): significant association of local coral cover with recent heat, non-significant
266 interaction with past heat.
- 267 - Group 3 (GR3): non-significant association of local coral cover with recent heat, significant
268 interaction with past heat.

269 - Group 4 (GR4): non-significant association of local coral cover with recent heat, non-significant
270 interaction with past heat.

271 For each survey, we computed the overall coral cover for every heat association group as the sum of
272 the taxa-specific coral cover of taxa assigned to every group. Next, we computed the models of
273 association with heat stress M21 and M28 for the overall coral cover of every heat association group
274 using the same methods described in the “Statistical analysis” section. The goal of these models was
275 to summarize average coral cover-heat associations for every heat association group. To visualize
276 such average associations, we used the VISREG R package (v. 2.7; Breheny and Burchett, 2017) and
277 custom R functions.

278 3 Results

279 3.1 Associations with long-lasting environmental trends

280 Most of the models (16 out of 24 models) that used long-lasting DHW trends as explanatory
281 variables (M1-M3) resulted in a stronger goodness-of-fit ($dAIC < -2$) when compared to a constant
282 null model and displayed significant ($p < 0.01$) negative associations ($\beta_{resp} < 0$) with coral cover
283 (Table 2A). These results were observed for models focusing on overall coral cover and for models
284 focusing on taxa-specific coral cover of branching (ACR.BRA), corymbose, tabular and digitate
285 Acroporidae (ACR.TCD), encrusting (POR.ENC) and massive (POR.MASS) Poritidae and
286 meandroid Favidae and Mussidae (FAV.MUS). In contrast, models of Pocilloporidae (POCI) and
287 branching Poritidae (POR.BRA) coral covers did not display significant associations with DHW
288 trends. In general, models accounting for average DHW (M1) showed a weaker goodness-of-fit
289 (higher values of $dAIC$), when compared with models based on maximal values of DHW (M3).

290 For models employing explanatory variables other than DHW, we generally observed weaker
291 goodness-of-fit and non-significant associations with coral cover variables (100 out of 112 models;
292 Table 2). Among the few exceptions were the following significant associations: maximal CHL with
293 coral cover of taxon ACR.TCD (M6 in Table 2A); SPM with overall coral cover and coral cover of
294 taxon POCI (M10-12); maximal SSS with overall coral cover (M15); and maximal SST with overall
295 coral cover and coral cover of taxa ACR.BRA, ACR.TCD and FAV.MUS (M18).

296 3.2 Associations with of period-specific trends of heat stress

297 Focusing on period-specific trends of heat stress, we observed that most models (52 out of 72
298 models) resulted in a stronger goodness-of-fit compared to a constant null model and displayed a
299 significant negative association between DHW trends and coral cover (Table 2B). The goodness-of-
300 fit generally appeared stronger in models based on DHW trends computed over shorter time periods
301 (e.g. 1 year; M19-21 in Table 2B) and using the maximal value as the trend-statistic (M21, M24,
302 M27). This was observed for overall coral cover and taxon-specific coral cover of taxa POR.ENC,
303 ACR.BRA, ACR.TCD and FAV.MUS. Similar to patterns observed for long-lasting trends of DHW,
304 no significant association with period-specific DHW trends were found for coral cover of taxa
305 POR.BRA and POCI.

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Table 2. Association models of coral cover with environmental trends. The table shows the coefficients of models associated with different coral cover variables (columns) with variables describing environmental trends (rows). Coral cover variables refer to overall coral cover 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), measured in field surveys. Environmental trends refer to the three statistics – mean, standard deviation and maximal value – applied to different variables: degree heating week (DHW), chlorophyll concentration (CHL), sea current velocity (SCV), suspended particulate matter (SPM), sea surface salinity (SSS) and sea surface temperature (SST). In table A), the models associate coral cover with long-lasting environmental trends, calculated across all the years prior to the survey date. In table B), models involve period-specific trends of DHW, measured over 1 year, 10 years or 20 years before the survey date. In table C), models involve two terms: (1) recent heat stress (maximal DHW measured during the year preceding the survey date) and (2) the interaction between recent heat stress and past heat stress (i.e. DHW statistics measured across all of the previous years). In table D), the median value (showing the interquartile range in parenthesis) of each coral cover variable ($MED_{coral\ cover}$) is shown, together with the coefficients of variation associated with the three random factors controlling for spatial autocorrelation of the survey locations (at a study area-level, $CV_{study\ area}$; at a regional-level, CV_{region} ; at a local-level, CV_{local}). $dAIC$ indicates the difference in the Akaike Information Criteria between each model and the null model (i.e. goodness-of-fit compared to the null model). In A) and B), β_{resp} shows the estimated effect in the unit scale of response variable (i.e. the percentage of absolute coral cover; negative effects are in red and positive effects are in green). In C), β_1 indicates the sign of the effect of recent heat stress on coral cover, and β_2 indicates the sign of the effect of the interaction between recent and past heat stress. Cells in grey indicate models failing to show (1) a stronger goodness-of-fit when compared to the null model and (2) β significantly ($p<0.01$) different from 0. The last column headed 'Env. range' shows the range of the environmental variable implicated in the association model, with the units indicated in parentheses. The complete list of the coefficients and statistics describing the association models are displayed in the Supplementary Table 1.

A) Univariate models of long-lasting environmental trends

	All		POR.BRA		POR.ENC		POR.MASS		ACR.BRA		ACR.TCD		POCI		FAV.MUS		Env. range
	$dAIC$	β_{resp}	$dAIC$	β_{resp}	$dAIC$	β_{resp}	$dAIC$	β_{resp}	$dAIC$	β_{resp}	$dAIC$	β_{resp}	$dAIC$	$\hat{\beta}_{resp}$	$dAIC$	$\hat{\beta}_{resp}$	
M1: DHW _{MEAN}	-18	-11.8±3	2	0.2±0.7	-3	-1.1±0.5	-7	-3.8±1.3	-12	-1.8±0.6	-9	-1.4±0.4	0	0.2±0.1	-3	0.2±0.1	0.01-0.93 [°C-wk]
M2: DHW _{STD}	-39	-4±0.6	1	-0.3±0.2	-10	-0.6±0.2	-17	-1.3±0.3	-21	-0.8±0.2	-15	-0.6±0.1	0	0±0	-10	-0.1±0.1	0.06-2.49 [°C-wk]
M3: DHW _{MAX}	-50	-0.4±0.1	-1	0±0	-19	-0.1±0	-16	-0.1±0.1	-26	-0.1±0	-12	-0.1±0.1	0	0±0	-15	-0.1±0.1	1.03-18.72 [°C-wk]
M4: CHL _{MEAN}	0	10.8±7.1	2	0.5±1.2	2	-0.5±0.8	-4	-4.3±1.8	-4	3.7±1.5	1	2.9±2.9	0	3.8±2.5	1	0.1±0.1	0.05-0.76 [mg/m ³]
M5: CHL _{STD}	2	1±10.7	1	3±2.8	2	-0.2±1.6	2	-1.2±2.9	1	3.6±3	2	-8.4±3.8	2	3.5±4.7	2	0±0.2	0.01-0.47 [mg/m ³]
M6: CHL _{MAX}	1	-0.9±0.9	1	0.2±0.2	2	0±0.1	2	0±0.2	2	0.1±0.2	-6	-0.6±0.2	0	0.3±0.4	2	0±0	0.09-4.34 [mg/m ³]
M7: SCV _{MEAN}	2	2.9±4.9	1	1.4±1.4	2	0.1±0.7	-2	5.1±2.6	1	-1±1.2	1	-2±2.2	2	0.1±0.4	2	0±0.2	0.04-1.4 [m/s]
M8: SCV _{STD}	2	-0.7±9.9	1	1.4±2	1	-0.7±0.9	0	5.3±3.6	2	-0.9±1.8	2	-1.1±3.4	2	-0.1±0.5	2	0.1±0.5	0.02-0.4 [m/s]
M9: SCV _{MAX}	2	-0.7±2	1	0.5±0.5	1	-0.2±0.2	1	0.8±0.8	2	0±0.4	2	0±0.8	2	0±0.1	2	0±0.1	0.1-2.0 [m/s]
M10: SPM _{MEAN}	-8	2.2±0.7	2	0.1±0.1	1	-0.1±0.1	2	0±0.1	0	0.2±0.2	0	0.7±0.4	-12	0.2±0.1	1	0±0	0.3-8.1 [g/m ³]
M11: SPM _{STD}	-10	4.5±1.3	2	0.1±0.2	1	-0.1±0.1	1	0.1±0.1	2	0.1±0.2	0	0.9±0.6	-23	0.5±0.1	2	0±0	0.1-5.1 [g/m ³]
M12: SPM _{MAX}	-6	0.5±0.2	2	0±0	1	0±0	2	0±0	2	0±0	-2	0.2±0.1	-30	0.1±0	2	0±0	0.9-34.3 [g/m ³]
M13: SSS _{MEAN}	-4	-3.4±1.3	1	-0.6±0.7	2	0±0.3	2	0.1±0.7	0	-0.3±0.2	0	0.7±0.5	1	0.1±0.2	-3	0.1±0.1	32.3-36.6 [%]
M14: SSS _{STD}	1	4.8±5.1	0	-1.7±1.2	1	0.9±1	2	-0.1±2.3	1	-0.7±0.7	2	-0.6±2.7	2	0.4±0.5	1	0.3±0.3	0.1-0.9 [%]
M15: SSS _{MAX}	-5	-4.5±1.6	-2	-1.5±0.7	0	0.3±0.2	2	0.4±0.7	2	-0.4±0.2	1	0.6±0.6	0	0±0.2	0	0.1±0.1	33.5-37.1 [%]
M16: SST _{MEAN}	1	2.9±1.7	2	0±0.2	-2	0.1±0.1	1	0.3±0.4	2	4.3±1.1	1	-0.4±0.3	1	0±0	0	0±0	23.0-29.2 [°C]
M17: SST _{STD}	2	-1.1±2.5	2	0.1±0.5	-2	-0.5±0.2	1	-0.9±1	2	0±0.2	2	0.3±0.5	1	-0.1±0.1	-3	0.1±0	0.4-3.1 [°C]
M18: SST _{MAX}	-36	-7.2±1.2	-1	-0.4±0.3	2	0±0.2	4	-1.1±0.4	-22	-3.8±0.7	-12	-1.4±0.4	0	0±0	-10	-0.2±0	27.3-30.8 [°C]

B) Univariate models of period-specific heat stress trends

	All		POR.BRA		POR.ENC		POR.MASS		ACR.BRA		ACR.TCD		POCI		FAV.MUS		Env. range	
	$dAIC$	β_{resp}	$dAIC$	β_{resp}	$dAIC$	β_{resp}	$dAIC$	β_{resp}	$dAIC$	β_{resp}	$dAIC$	β_{resp}	$dAIC$	$\hat{\beta}_{resp}$	$dAIC$	$\hat{\beta}_{resp}$		
M19: DHW _{MEAN_1yr}	-71	-1.2±0.1	2	0±0	-30	-0.2±0	-7	-0.2±0.1	-27	-0.2±0	-23	-0.1±0	2	0±0	-13	-0.1±0	0-4 [°C-wk]	
M20: DHW _{STD_1yr}	-72	-0.9±0.1	0	0±0	-32	-0.1±0	-5	-0.2±0.1	-29	-0.1±0	-24	-0.1±0	2	0±0	-13	-0.02±0	0-5.6 [°C-wk]	
M21: DHW _{MAX_1yr}	-74	-0.4±0	1	0±0	-33	-0.1±0	-3	-0.1±0	-29	-0.1±0	-25	-0.1±0	2	0±0	-13	-0.01±0	0-13.8 [°C-wk]	
M22: DHW _{MEAN_10yrs}	-31	-4.1±0.7	2	0±0.2	-10	-0.6±0.2	-6	-1.3±0.5	-15	-0.6±0.2	-14	-0.6±0.2	0	0.1±0	-5	-0.1±0	0.01-2.1 [°C-wk]	
M23: DHW _{STD_10yrs}	-56	-2.2±0.3	-0.1±0.1	19	-0.3±0.1	-8	-0.5±0.2	-23	-0.4±0.1	-29	-0.4±0.1	-29	-0.4±0.1	2	0±0	6	-0.05±0	0.04-3.8 [°C-wk]
M24: DHW _{MAX_10yrs}	-65	-0.4±0	0	0±0	-27	-0.1±0	-6	-0.1±0	-29	-0.1±0	-35	-0.1±0	2	0±0	-7	-0.01±0	0.3-18.7 [°C-wk]	
M25: DHW _{MEAN_20yrs}	-20	-7.4±1.6	2	0.1±0.5	-6	-0.9±0.3	-5	-2.2±0.9	-13	-1.2±0.4	-10	-1±0.3	0	0.1±0	-3	-0.1±0.1	0-1.2 [°C-wk]	
M26: DHW _{STD_20yrs}	-44	-3.1±0.5	-0.1±0.2	-14	-0.5±0.1	-14	-0.9±0.2	-24	-0.6±0.1	-16	-0.4±0.1	-2	0±0	-9	-0.07±0	0.1-2.8 [°C-wk]		
M27: DHW _{MAX_20yrs}	-52	-0.4±0.1	2	0±0	-20	-0.1±0	-16	-0.1±0	-28	-0.1±0	-12	-0.05±0	2	0±0	-14	-0.01±0	1-18 [°C-wk]	

C) Bi-variate models of interactions between recent and past heat stress																									
	All		POR.BRA		POR.ENC		POR.MASS		ACR.BRA		ACR.TCD		POCI		FAV.MUS		Env. range								
	dAIC	β_1	β_2	dAIC	β_1	β_2	dAIC	β_1	β_2	dAIC	β_1	β_2	dAIC	β_1	β_2	dAIC	β_1	β_2							
M28: $DHW_{MEAN_>1yr}$	0	-	+	0	-	+	1	-	-	1	-	+	-4	-	+	-18	-	+	-36	-	+	1	-	-	0-0.9 [°C-wk]
M29: $DHW_{STD_>1yr}$	0	-	+	1	-	+	2	-	+	-2	-	+	0	-	+	-3	-	+	-20	-	+	2	-	-	0.02-2.5 [°C-wk]
M30: $DHW_{MAX_>1yr}$	0	-	+	1	-	+	2	-	+	0	-	+	2	-	+	2	-	+	-8	-	+	2	-	+	0.1-18 [°C-wk]

D) Coral cover and spatial variation																		
	All		POR.BRA		POR.ENC		POR.MASS		ACR.BRA		ACR.TCD		POCI		FAV.MUS			
$MED_{coral\ cover}$	15.5(7-24)%	0.5(0.1-1.4)%	0.1(0-0.5)%	1.7(0.7-4.1)%	0.5(0.2-1.6)%	1.4(0.6-3.4)%	1(0.2-2.9)%	0.3(0-1.6)%										
$CV_{study\ area}$	0.444±0.043	0.175±0.014	0.168±0.043	0.173±0.011	0.021±0.057	0.085±0.037	0.164±0.016	0.226±0.02										
CV_{region}	0.202±0.035	0.054±0.003	0.04±0.014	0.103±0.004	0.098±0.01	0.122±0.014	0.072±0.005	0.032±0.006										
CV_{local}	0.198±0.014	0.054±0.004	0.001±0.001	0.104±0.003	0.099±0.005	0.105±0.011	0.085±0.005	0.036±0.003										

308

309 3.3 Interactions between recent and past heat stress

310 Regarding the bi-variate models, we observed that models accounting for the interaction of recent
311 heat stress with average DHW trends over the long-term (M28) showed a stronger goodness-of-fit
312 (when compared to the null models) for coral cover of taxa ACR.BRA, ACR.TCD and POCI. For
313 these models, the association between recent heat stress and coral cover was of negative sign, and
314 this negative association was contrasted by the interaction of positive sign with long-term heat stress.
315 The same results were observed for coral cover of taxon POCI in models accounting for standard
316 deviation and maximal DHW trends over the long-term (M29 and M30, respectively).

317 3.4 Sorting taxa by heat associations

318 We sorted taxa into four groups showing distinct types of heat associations (Figure 3).

319 Group 1 (GR1) included ACR.BRA and ACR.TCD; these were the taxa that showed a negative
320 association between coral cover and recent heat stress ($p < 0.01$; $dAIC < -2$), which was
321 significantly modulated by the interaction with past heat stress. The association models for GR1
322 showed local differences in coral cover of -0.11 ± 0.02 % per °C-week of DHW_{MAX_1yr} (Figure 3A,
323 purple regression line). In GR1, the local differences in coral cover associated with recent heat stress
324 appeared to be mitigated at locations with higher past heat stress (Figure 3B, top-left graph). For
325 example, a DHW_{MAX_1yr} of 1°C-week corresponded to a local difference in coral cover of $-0.20 \pm$
326 0.03 % in locations where average past heat stress ($DHW_{MEAN_>1yr}$) was below 0.3°C-week,
327 whereas a difference in coral cover of -0.07 ± 0.01 % was observed in locations where average past
328 heat was above 0.5°C-week.

329 Group 2 (GR2) included taxa that had a significant negative association between coral cover and
330 recent heat stress, but without a significant modulation of the interaction with past heat stress. This
331 group included the taxa POR.MASS, POR.ENC and FAV.MUS. The association model for GR2
332 showed local differences in coral cover of -0.05 ± 0.01 % per °C-week of DHW_{MAX_1yr} (Figure 3A,
333 orange regression line). Accounting for the modulating interaction with past heat stress did not
334 improve the goodness-of-fit ($dAIC > -2$) of the models when compared to the univariate
335 counterpart accounting only for recent heat stress (Figure 3B, top-right graph).

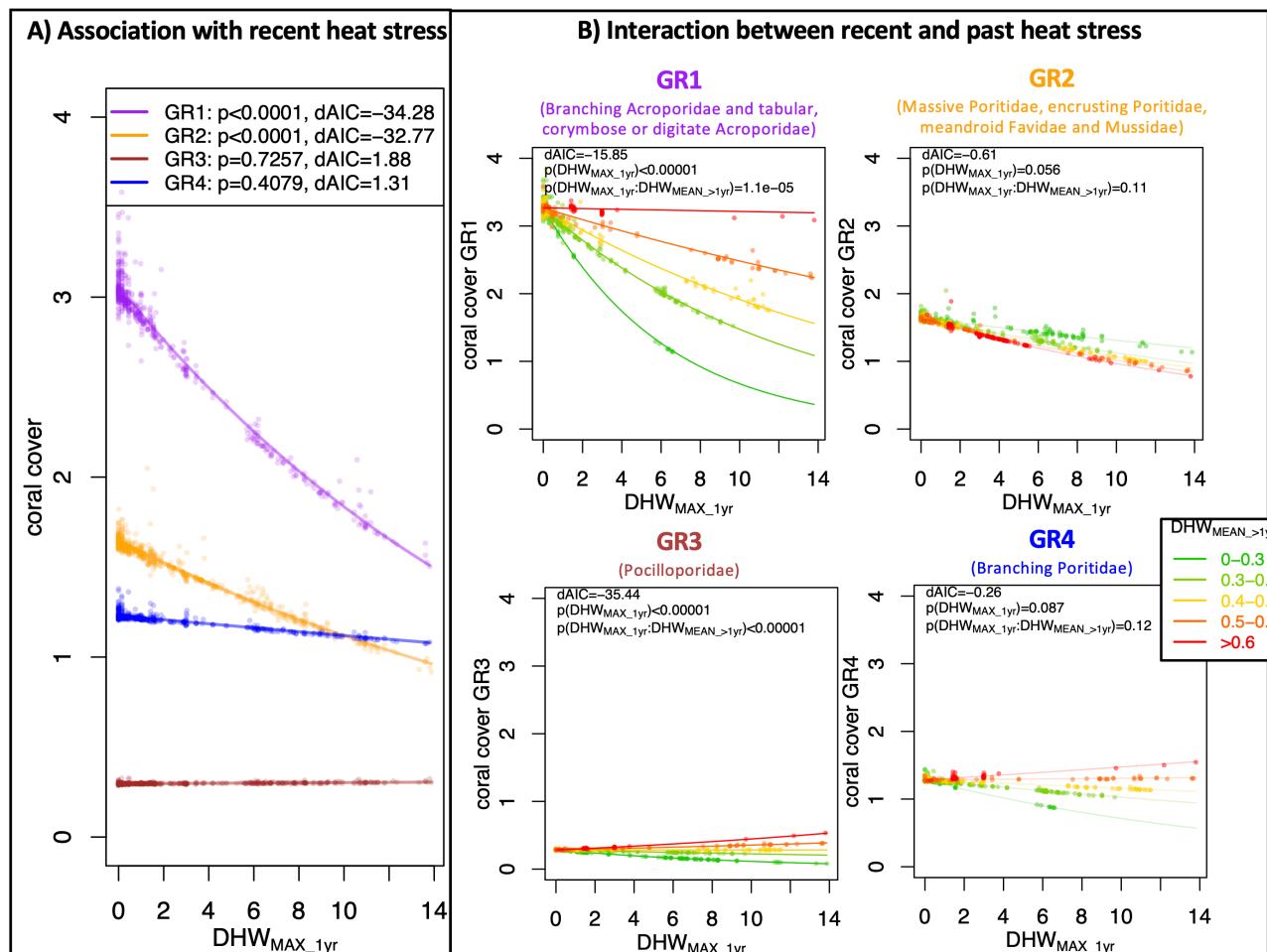
336 Group 3 (GR3) included the POCI taxon alone. Here, significant differences in coral cover associated
337 with recent heat stress were only detected when accounting for the modulating interaction with past

338 heat stress. Indeed, the univariate model that only accounted for recent heat stress did not improve
339 the goodness-of-fit ($dAIC > -2$) when compared to a constant null model (Figure 3A, brown
340 regression line). However, the bi-variate model showed significant changes in the association
341 between coral cover and recent heat stress, and such changes followed past heat stress levels (Figure
342 3B, bottom-left graph): when past heat stress was low, recent heat stress showed a negative
343 association with coral cover, whereas when past heat stress was high, the association between coral
344 cover and recent heat stress was of positive sign. For example, a DHW_{MAX_1yr} of 1°C-week
345 corresponded to local differences in coral cover of $-0.014 \pm 0.002\%$ when average past heat stress
346 ($DHW_{MEAN_>1yr}$) was below 0.3°C-week, whereas it corresponded to local differences in coral cover
347 of $+0.007 \pm 0.001\%$ when average past heat stress was above 0.5°C-week.

348 Group 4 included the POR.BRA taxon alone, where no significant differences in coral cover were
349 detected in association with recent heat stress, nor with a modulating interaction of past heat stress
350 (Figure 3A, blue regression line; Figure 3B, bottom-right graph).

351

Figure 3. Groups of coral cover-heat stress associations. The plots display the associations between local coral cover and heat stress trends at survey sites for the four groupings of taxa with similar heat responses (heat association groups): in Group 1 (GR1, purple), taxa coral cover is associated with recent heat stress, where this association interacts with past heat stress; in Group 2 (GR2, orange), coral cover is associated with recent heat stress, without significant interaction with past heat stress; in Group 3 (GR3, brown), recent heat stress alone is not significantly associated with taxa coral cover, but the interaction between recent and past heat stress shows a significant association with coral cover; and in Group 4 (GR4, blue), no significant association between coral cover and heat stress was found. Plot A) displays the association of coral cover with recent heat stress, measured as the maximal degree heating week measured during the year before the survey (DHW_{MAX_1yr}), for each of the four groups. Plots in B) show the association of coral cover with recent heat stress, for survey locations exposed to different levels of past heat stress, measured as the average DHW during all the previous years ($DHW_{MEAN_>1yr}$). 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.



355 **4 Discussion**

356 **4.1 Local differences in coral cover mirror heat stress trends**

357 We observed that survey sites exposed to elevated long-lasting and period-specific trends of Degree
358 Heating Week (DHW) almost systematically displayed lower levels of coral cover than expected
359 locally. These observations are consistent with previous studies where DHW-related variables were
360 used as proxies for heat stress when investigating associations with coral decline or bleaching
361 severity (Hughes et al., 2018; Head et al., 2019; McClanahan et al., 2019; Babcock et al., 2020). For
362 the other environmental variables examined here (chlorophyll concentration, sea current velocity,
363 suspended particulate matter, sea surface salinity and sea surface temperature), the associations with
364 local differences in coral cover were generally weaker and seldom significant. As these
365 environmental constraints were expected to drive local differences in coral cover based on past
366 studies (Hédouin et al., 2015; Riegl et al., 2015; Jones et al., 2020; Sully and van Woesik, 2020), it is
367 possible that the variables that we used are not appropriate proxies of such environmental constraints,
368 particularly at the depth at which coral cover surveys were performed (see the “Limitations” section).

369 When we decomposed the effects of DHW into period-specific trends, we observed that association
370 models with coral cover employing distinct DHW statistics (mean, standard deviation, and maximal
371 value) as explanatory variables often displayed substantial differences in the goodness-of-fit. These
372 results must be considered with care, due to the high collinearity (often > 0.8) between distinct DHW
373 statistics measured during the same period (Supplementary Figure 1). Nevertheless, we note that
374 univariate models employing DHW variables based on maximal values systematically provided a
375 higher goodness-of-fit for the associations with coral cover, when compared to univariate models
376 employing DHW averages or standard deviations. In the significant bi-variate models, we observed
377 that reefs exposed to low levels of past heat stress showed a stronger negative association between
378 coral cover and recent heat stress, compared to reefs exposed to higher levels of past heat stress. In
379 contrast to univariate models, here this mitigating role of past heat was better explained by DHW
380 averages than by DHW maximal values or DHW standard deviations. Average DHW might therefore
381 represent the frequency of past heat stress that previous research found to be associated with decrease
382 in bleaching rates (Thompson and van Woesik, 2009).

383

384 **4.1 Taxon-specific heat associations**

385 We classified coral taxa into four groups based on the patterns of coral cover association with recent
386 and past heat stress.

387 Local differences in coral cover for taxa in Groups 1 (GR1) and 2 (GR2) matched the variation of
388 recent heat stress, where reefs exposed to higher recent heat stress had lower coral cover than locally
389 expected. The magnitude of this negative association was twice as strong for GR1 than for GR2.
390 Assuming that these associations describe a causal relationship (i.e. recent heat stress drives local
391 loss of coral cover), such differences between GR1 and GR2 might reflect differences in heat
392 sensitivity. Indeed, GR1 includes heat sensitive taxa such as branching, corymbose and tabular
393 *Acropora* and *Montipora*, while GR2 includes stress tolerant taxa such as massive and encrusting
394 Poritidae, and meandroid Faviidae and Mussidae (Loya et al., 2001; Darling et al., 2012; Guest et al.,
395 2016; Hughes et al., 2018; Pisapia et al., 2019).

396 For coral taxa of heat association Groups 3 (GR3) and 4 (GR4), local differences in coral cover was
397 not associated with variation in recent heat stress. However, previous studies listed taxa from these
398 groups (GR3: Pocilloporidae, GR4: branching Poritidae) as “heat sensitive” (Loya et al., 2001; Guest
399 et al., 2016) and “long-term losers” of coral bleaching (van Woesik et al., 2011). If the causal
400 relationship assumed above were true, we expect that reefs exposed to higher recent heat stress would
401 have lower coral cover for these taxa, compared to reefs exposed to lower recent heat. In fact, this
402 negative association between coral cover of these taxa and recent heat stress was observed, but as we
403 discuss below, it is only visible when considering the interaction with past heat stress.

404 When considered with the interaction with past heat stress, the association between coral cover and
405 recent heat stress showed distinct patterns for the four heat association groups. For GR1, the negative
406 association between coral cover and recent heat stress appeared to be mitigated by the interaction
407 with past heat stress. This means that reefs exposed to high recent heat stress displayed lower coral
408 cover than locally expected; however, among these reefs, those frequently exposed to past heat stress
409 had relatively higher coral cover compared to reefs less frequently exposed. Of note, reefs exposed to
410 very frequent past heat stress ($DHW_{MEAN_>1yr} > 0.6^{\circ}C - week$) displayed similar coral cover
411 regardless of recent heat stress exposure. GR3 had a similar, yet stronger, interaction as was observed
412 for GR1. Indeed, in GR3 there was a negative association between coral cover and recent heat stress
413 for reefs exposed to lower frequency of past heat stress, yet a positive association for reefs exposed to
414 higher frequency of past heat stress. These results are consistent with previous local observations of
415 taxa from these groups (*Acropora* and *Pocillopora*) that showed increased heat resistance after
416 previous thermal exposure (Guest et al., 2012; McClanahan, 2017).

417 Similar increase in heat resistance was also previously observed for branching *Porites* (McClanahan,
418 2017). We found that GR4 (which includes branching Poritidae) showed similar associations and
419 interactions to GR3, though these models were not found to be significant. The lack of clear
420 statistical signal in these associations might be due heterogenous heat responses among species from
421 GR4. For GR2 too, the interaction with past heat did not result as significant, but here the patterns
422 were completely different from the other groups. Indeed, the interaction with past of heat was of
423 negative sign, suggesting that past heat stress reinforced the negative association between recent heat
424 stress and coral cover.

425 One possible explanation is based on the assumption that the associations between coral cover and
426 heat stress are causal relationships, i.e. that recent heat stress exposure can drive local coral cover
427 loss, and frequent exposure to past heat stress can provide a protection against such loss. Under this
428 assumption, GR1, GR3 and some species in GR4 might have changed their thermal sensitivity in
429 response to heat stress exposure over the past three decades. There are at least three (not mutually
430 exclusive) phenomena that could underpin such rapid responses. The first phenomenon is a shift at
431 the community level, where heat sensitive species have been progressively replaced by heat tolerant
432 species from the same heat association group. This hypothesis assumes that there are substantial
433 differences in heat tolerance between species from GR1 and GR3, which is possible even though
434 corals within each of these groups usually have similar life-history traits and heat sensitivities (Loya
435 et al., 2001; van Woesik et al., 2011; Darling et al., 2012). A second possible explanation is
436 evolutionary adaptation, where colonies carrying genetic traits linked to thermal tolerance have been
437 positively selected by recurrent exposure to heat stress. Indeed, recent environmental-genomics
438 studies have suggested that the selection of such genetic traits could occur across relatively short time
439 periods (~30 years) in both *Acropora* and *Pocillopora* species (Selmoni et al., 2020b, 2021).
440 Nevertheless, this interpretation is hampered by the fact that every heat association group is
441 composed of multiple species, and that each species likely has distinct adaptive potentials. The last

442 phenomenon that could explain a hypothetical response to past heat exposure is physiological
443 acclimation, where individuals exposed to past heat stress progressively adjust their metabolism, thus
444 becoming more heat tolerant. However, acclimation is unlikely to play a key role here, as it usually
445 occurs through constant heat stress exposure (e.g. large daily variation of SST; Palumbi et al., 2014),
446 rather than via sporadic/seasonal heat exposure (i.e. decadal frequency of thermal anomalies).

447

448 4.2 Limitations

449 In this study, we investigated the associations between local coral cover and a set of environmental
450 constraints measured with remote sensed data. This approach is inevitably exposed to bias because
451 the spatial resolution of the environmental variables we employed is coarse (between 5 to 8 km), in
452 comparison to the size of the transects providing the coral cover data (up to 2 km). The consequence
453 of this mismatch in spatial resolutions is that habitat types (e.g., reef slope vs. reef flat) are
454 overlooked by our analysis. Furthermore, the coral cover data that we employed was systematically
455 collected at 10 meters of depth, such that our analyses might not be representative for coral cover at
456 other depths.

457 Additionally, previous studies pointed out that geographic position is a key element for explaining
458 variation in coral cover and bleaching responses (McClanahan et al., 2019; Sully et al., 2019). Our
459 work is not an exception to this, as the random factors used to account for spatial autocorrelation
460 among survey sites controlled for a substantial part of coral cover variation. This suggests that there
461 are important factors proxied by geographical position that were not explicitly accounted for in our
462 analyses. Such factors could be environmental conditions that we did not consider; or be
463 environmental conditions that we did consider, but for which alternative types of descriptors should
464 have be used. For instance, recent studies proposed measures of heat stress that are complementary to
465 DHW, such as statistics describing SST bimodality and spell peaks (McClanahan et al., 2019,
466 2020a). The same reasoning applies to the modulation of heat stress by non-heat related
467 environmental conditions (such as tidal range, cyclone frequency, human population density), which
468 were found in previous works (Maina et al., 2011; Safaei et al., 2018; McClanahan et al., 2019,
469 2020a, 2020b; Sully et al., 2022) but that wasn't the focus of the current study.

470 Finally, we used taxonomic groups primarily defined by taxonomic family and growth form and
471 assumed that species belonging to each of these taxa had similar associations with environmental
472 trends. In reality, this might not necessarily be the case, as it is possible that within these taxa there
473 are species with divergent heat associations. Furthermore, it is important to underline that each heat
474 association observed is an average for a given taxon, and that for this average we are not able to
475 evaluate the specific weight of single species. Future work could focus on re-annotating the CSS
476 surveys with more specific taxonomic labels (for instance, at the genus level), so that the analyses
477 can be refined with a higher taxonomic resolution.

478 4.3 Perspectives

479 We observed that local differences in coral cover matched distinct patterns of interaction between
480 recent and past heat stress depending on taxa. These distinct patterns could highlight differences in
481 how taxa respond to past exposure to heat stress, and future work should investigate the possible
482 causes.

483 As discussed above, one possible cause is a community shift from heat sensitive to heat tolerant
484 species. To evaluate this hypothesis, future studies could focus on field survey data at higher
485 taxonomic resolution than in our analysis, to allow heat associations to be assessed at a species level.
486 Such studies are likely to be hampered by difficulties in defining coral species based on visual
487 surveys (Postaire et al., 2016; Forsman et al., 2020; Oury et al., 2020; Prada and Hellberg, 2021;
488 Rippe et al., 2021). This could be overcome by using molecular surveying techniques such as
489 environmental DNA, which could make it possible to establish objective molecular boundaries to
490 distinguish between surveyed species (Shinzato et al., 2018, 2021; Dugal et al., 2022).

491 These presumptive responses to past heat exposure could also be mirroring micro-evolutionary
492 processes, where individuals with genetic traits conferring thermal tolerance are persisting after
493 recurrent heat exposure. To investigate this, population genomic studies featuring genotype-
494 environment association analyses could be performed to evaluate the emergence of adaptive genetic
495 traits at reefs exposed to heat stress over the past decades (Riginos et al., 2016; Selmoni et al., 2020b,
496 2021).

497 Another possible mechanism underpinning these association with past heat is the physiological
498 acclimation of corals exposed to recurrent thermal stress. This phenomenon could be verified by
499 performing standardized and systematic eco-physiological analyses, which can be done using
500 portable experimental systems to test heat tolerance (e.g. the Coral Bleaching Automated Stress
501 System, CBASS; Voolstra et al., 2020).

502 In reality, it is likely that each of the three phenomena discussed here act together in concert to shape
503 the heat response of a reef exposed to recurrent thermal stress. Understanding and disentangling the
504 individual contribution of each phenomenon will be aided by running trans-disciplinary studies (i.e.,
505 performing ecological surveys, genomic and eco-physiological analyses in parallel) across the same
506 reef system.

507 4.4 Conclusions

508 We performed an association study across reefs worldwide that revealed differences in local coral
509 cover associated with heat stress trends. These associations differed between coral taxa, which we
510 sorted into four groups accordingly:

511 **- Group 1: Branching, corymbose, tabular and digitate Acroporidae.** Reefs exposed to recent
512 heat stress displayed lower coral cover than locally expected; among these reefs, those previously
513 exposed to frequent past heat stress showed relatively higher coral cover, when compared to those
514 less frequently exposed.

515 **- Group 2: Massive and encrusting Poritidae and meandroid Faviidae and Mussidae.** Reefs
516 exposed to recent heat stress displayed lower coral cover than locally expected, yet this association
517 was weaker than for Group 1. No mitigating interaction of recent heat stress with past heat stress was
518 observed.

519 **- Group 3: Branching Pocilloporidae.** The spatial overlap between differences in local coral cover
520 and recent heat stress was only observed when considering the interacting role of past heat stress.
521 Indeed, reefs exposed to frequent past heat stress showed a positive association between recent heat
522 stress and coral cover, while a negative association was observed when past heat stress was less
523 frequent.

524 - **Group 4: Branching Poritidae.** The associations between coral cover and heat stress trends
525 appeared to follow a similar trend to Group 3, although this was weaker, noisier and not statistically
526 significant.

527 The groupings presented here could represent coral taxa-specific response to heat stress exposure
528 across reefs worldwide over the past two to three decades. Future studies will need to validate the
529 existence of such processes and investigate their nature (community shifts, evolution or acclimation)
530 in further depth and at higher resolutions.

531 5 Conflict of Interest

532 *The authors declare that the research was conducted in the absence of any commercial or financial
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