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REPORT

Branching coral growth and visual health during bleaching and recovery on the central Great Barrier Reef

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Abstract Coral reefs are under threat from cumulative impacts such as cyclones, crown-of-thorns starfish (COTS) outbreaks and climate-driven coral bleaching events. Branching corals are more severely impacted by these events than other coral morphologies due to their sensitivity to heat stress and weaker skeletons and COTS preferred prey. The central Great Barrier Reef experienced unprecedented back-to-back bleaching events in 2016 and 2017. This study commenced in 2017 at the peak of heat stress and examined the impact of the heatwave on the survival and recovery of corals by assessing the growth, health (based on the visual health index) and physiological parameters (chlorophyll a, zooxanthellae density, lipid and protein content) of two species, *Acropora millepora* and *Pocillopora acuta* ($N = 60$ colonies for each species). It was conducted across a gradient of turbidity at three reefs, Pandora, Orpheus and Rib, that experienced in April 2017, degree heating weeks (DHW) of 9, 8 and 7, respectively. Orpheus experienced the worst bleaching, based on visual health score, followed by Rib and Pandora. Rib experienced the greatest mortality (78% by Nov 2017); however, this was attributed to the presence of actively feeding crown-of-thorns starfish. Growth rates of *A. millepora* were almost twice the rate of *P. acuta*. Both species showed significant seasonal variation with growth of *A. millepora* and *P. acuta* 35–40% and 23–33% significantly greater in the summer, respectively. Differences in growth rates were best explained by indicators of energy acquisition. For example, the most important predictor variable in determining higher growth rates and visual health score in *A. millepora* was chlorophyll a content. For *P. acuta*, visual health score was the best predictor variable for higher growth rates. This study highlights the important role that chlorophyll a and associated symbionts play in growth and survival in these corals during and after a heat stress event.

Keywords Heat stress · Acropora · Pocillopora · Chlorophyll

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Introduction

Coral reefs are highly biodiverse ecosystems and under threat from increased frequency of anthropogenic disturbances such as rising temperatures, pollution and sedimentation (Hoegh-Guldberg 2011; Hughes et al. 2018). This is of concern as coral reefs are a major food source for a large proportion of the global population, provide considerable economic benefits and house a large proportion of

the world's marine biodiversity (Cesar et al. 2003). Even large well-connected coral reef systems such as Australia's Great Barrier Reef (GBR) are at risk from more frequent heatwaves as the global climate system responds to increasing greenhouse gases. There have now been four mass bleaching events recorded on the GBR in the last five years, the unprecedented back-to-back bleaching events in 2016 and 2017 and again in 2020 and 2022 (GBRMPA 2022).

Bleaching susceptibility varies among geographical locations, species and individual corals (Grottoli et al. 2004). Bleaching extent of corals is influenced by environmental conditions such as turbidity (Anthony et al. 2007), nutrient availability (Rodrigues and Grottoli 2007) and water temperature (Heron et al. 2016; Hughes et al. 2018; Lough et al. 2018). Among coral species, faster growing species such as *Acropora* spp and *Pocillopora* spp are typically more sensitive to heat stress and are therefore more vulnerable to bleaching(Loya et al. 2001; Darling et al 2013) with higher mortality rates than massive corals such as *Porites* spp (Guest et al. 2012; Baum et al. 2023). Among individuals, bleaching susceptibility is regulated by underlying physiological mechanisms (Dunn et al. 2012; Grottoli et al. 2006). A shift to more thermally resistant *Symbiodiniaceae* (Berkelmans and van Oppen 2006; Rowan 2004, LaJeunesse et al. 2018), the use of lipid reserves (Anthony et al. 2009) and heterotrophy (Anthony and Fabricius 2000) are some of the mechanisms that determine individual resistance and resilience to heat stress (Gates and Edmund 1999; Maynard et al. 2008).

Coral bleaching occurs when the endosymbiotic photosynthetic dinoflagellates (Zooxanthellae, *Symbiodiniaceae* spp.) are expelled by the coral host due to stress. Although there are various sources of stress that can result in bleaching, since the 1980s large-scale mass coral bleaching events have been linked to thermal stress during extreme heat waves (Glynn 1993; Heron et al. 2016; Lough et al. 2018). As a result of the loss of the symbionts, the coral tissue loses its pigmentation provided by the symbiont, becoming translucent, revealing the white skeleton beneath, giving the appearance of being "bleached". The carbon by-products of photosynthesis produced by the symbionts can provide ∼ 90% of the energy requirements of the coral host (Grottoli et al. 2006; Jones et al. 2008). As a result, disruption of the provision of nutrients to the corals can lead to starvation and to reductions in skeletal tissue growth, calcification, and fecundity while increasing the susceptibility to disease and mortality (Kemp et al. 2014; Heron et al. 2016; Hughes et al. 2017; Grottoli et al. 2018). Bleached corals can recover and regain their symbionts if the heat stress is not too intense or too prolonged (Grottoli et al. 2006). In addition, symbiont shuffling during elevated temperature from sensitive to more thermotolerant

symbionts allowed some corals to recover even during a heat stress event (Claar et al. 2020).

For all organisms, the exchange of energy regulates physiological processes, including maintenance, growth and reproduction, which determine survival and fitness (Maltby 1999). The energetic dynamics of corals are determined by the symbiotic relationship between the coral host and symbiont. The *Symbiodiniaceae* fix carbon, which is transferred to the host coral as an energetic source (Muller-Parker et al. 2015). The excess carbon is stored as lipids or excreted as mucus (Anthony and Fabricius 2000, Cooper et al. 2011). When the carbon fixed by the *Symbiodiniaceae* is insufficient for the respiration for both organisms, energy may be provided by alternative sources (Muller-Parker et al. 2015) including: lipid reserves (Anthony et al. 2009; Rodrigues and Grottoli 2007) and/or heterotrophy by the host (Grottoli et al. 2006, 2018; Anthony et al. 2009; Schoepf et al. 2013). Therefore, the dynamics of the available energy will determine the content of high-energy reserves (lipid, protein and carbohydrates) (Anthony et al. 2009; Muller-Parker et al. 2015). Corals with greater energy reserves and more thermally resistant endosymbionts may have the capacity to acclimatise to thermal stress (Grottoli et al. 2014).

Fast coral growth is also a key factor in the recovery of reefs after disturbance (Smith et al. 2008, Jones and Berkelmans 2010). *Acropora millepora and Pocillopora acuta* are fast-growing, habitat generalist, branching coral species (Pratchett et al. 2015), with low tolerance for heat stress (Maynard et al. 2008; Guest et al. 2012). The faster growth of these corals allows for quicker recover from physical damage or bleaching events and they have displayed an increase in tolerance from recurrent bleaching events (Guest et al. 2012) possibly by modification of their zooxanthellae (Rowan 2004; Berkelmans and van Oppen 2006) and/or by regulation of the host physiology (Baird et al. 2009).

The objective of this study was to assess the health, growth and physiological parameters (chlorophyll *a,* zooxanthellae density, protein, and lipid content) of branching coral species *A. millepora* and *P. acuta* during and throughout a year after the 2017-bleaching event on the central GBR. The term "health" is used throughout the manuscript in reference to the standardised Coral Watch health charts that measures the pigmentation of a coral colony based on the shade of colour from the chart and reflects visual health (Siebeck et al. 2006). However, invasive sampling of physiological condition is needed to determine overall health of a coral and needs to be ground-truthed in a specific region to capture the range of colour for healthy and bleached corals (e.g. Bahr et al. 2020). The study was carried across three locations on the central GBR: Pandora Reef, Orpheus Island, Rib Reef. Monitoring of individual corals (April 2017–April 2018) was used to quantify visual health (using standardised health charts), growth and physiology of these species, and

investigate via in situ sampling the effects of thermal stress and post-stress survival and recovery. We were specifically interested in:

- How does growth differ through time, species, location and what is the key indicator for greater growth rates during and after bleaching events?
- What physiological parameters influence higher survival and greater growth post-bleaching events? Does higher lipid and chlorophyll *a* content play a key role as previously hypothesised?
- Visual health score cards had been standardised based on chlorophyll and symbiont density (Siebeck et al. 2006), but does the composition of other physiological traits (protein, lipids) also play a role in determining the visual health score?

Methods

Study Sites

To investigate temporal dynamics of coral growth and physiology during recovery from bleaching, visual health of colonies of *A. millepora* and *P. acuta* was monitored *in situ* via photogrammetry and branches collected across three locations (two sites per location): Pandora Reef (Site A -18.81199S, 146.43138E, Site B -18.81177S, 146.42911E), Orpheus Island (Site A -18.64603S, 146.48991E, Site B -18.64276S, 146.49142E), and Rib Reef (Site A: -18.47986S, 146.86588E, Site B: 18.47972S, 146.86740E). These central GBR sites are located across a turbidity gradient due to summer freshwater flood plumes containing sediment from the mainland (Fig. S1). Pandora Reef (located on the boundary of a sediment wedge) and Orpheus Island (outside of the sediment wedge) are positioned inshore, while Rib reef is located on the midshelf (Anthony 2000). The inshore reefs are seasonally influenced by Burdekin River runoff, which enters the GBR south of Townsville

whereas Rib is only affected by extreme freshwater flood events (Fabricius et al. 2014). To avoid confounding bias, sampled corals were selected only on the leeward side in depths of < 4 m. The study coincided with an outbreak of crown-of-thorns starfish (COTS) at Rib Reef, so corals were tagged at 3–4 m depth to minimise COTS predation on the sampled corals while maintaining comparable sampling depth across locations.

Environmental conditions

Sea-surface temperature (SST) data were acquired from the NOAA Coral Reef Watch (CRW) CoralTemp product (see Skirving et al. 2019, 2020) and daily time-series extracted at the study locations (Fig. S1). Heat stress for the period 2015–2020 was calculated using the Degree Heating Weeks (DHW) metric, following the standard CRW algorithm that accumulates temperature anomalies that are at least 1 °C above the climatological summertime maximum temperature (Liu et al. 2014; Heron et al. 2014).

Coral sampling

In April 2017, 120 colonies (60 *A. millepora* and 60 *P. acuta*) were tagged (Table 1) and photographed with a coral health chart and reference scale (Fig. 1). They were photographed with a Canon G7 camera at each time point to obtain data on coral health and mortality (see details below). Selected corals were evenly distributed at each location, two sites (A, B) at each reef, and with colony size ranging from 10 to 55 cm maximum diameter (*n* = 10 colonies per site per species). In order to re-locate sampled corals, cattle tags were placed in the vicinity of the coral so as not to disrupt growth. After four weeks (May 2017), re-sampling was carried out to collect two branches from each colony for physiology and take another coral health photo. Collected coral branch fragments were snap frozen with liquid nitrogen and stored in a dewar immediately after collection to preserve tissue physiology, transported to the Australian Institute of

Table 1 Total number of corals (N) sampled at Orpheus, Pandora and Rib of *A. millepora* and P. acuta in April 2017, May 2017, November 2017, and April 2018

Species	Location	April 2017			May 2017			Nov 2017			April 2018		
		N	Dead	NS	N	Dead	NS	N	Dead	NS	N	Dead	NS
A. millepora	Pandora	20	–	–	18*	–	–	18	–	–	17	–	1
	Orpheus	20	–	–	17	3	–	9	11	–	6	11	3
	Rib	20	–	–	17	3	–	1	19	–	–	19	1**
P. acuta	Pandora	20	–	–	20	–	–	19	–	1	14	–	6
	Orpheus	20	–	–	20	–	–	19	1	–	9	2	9
	Rib	20	–	–	15	5	–	10	10	–	–	10	10**

NS not sampled as colonies could not be re-located

*Two corals of *A. millepora* were incorrectly identified and not included further in the study. **Collection trip to Rib in 2018 did not occur
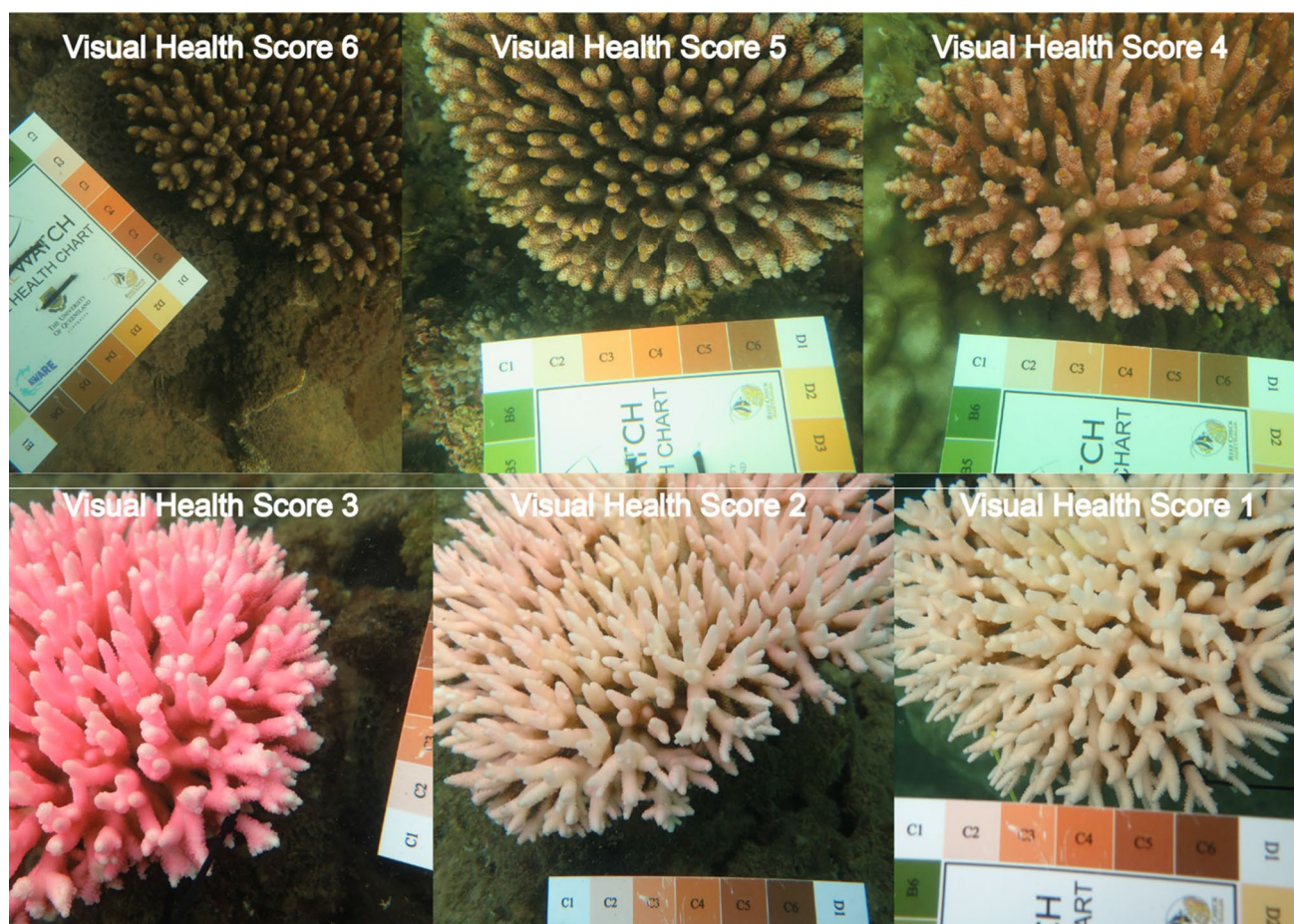
Fig. 1 The spectrum of bleaching experienced by *A. millepora* corals on the central Great Barrier Reef in April 2017. Round visual health scores determined from health charts displayed on the image

Marine Science (Townsville), and stored at − 80 °C until processing. Dead colonies were noted but not re-sampled (Table 1).

Before the onset of austral summer, a third trip took place in November 2017 to document recovery over austral winter when the water is cooler. Coral health was re-assessed by photographing each colony alongside the coral health chart and a reference scale (Fig. 1), and another two branches from each colony were collected. One colony at Pandora Reef could not be re-located and so was not sampled (NS in Table 1). Due to the high incidence of mortality recorded at Rib Reef, no subsequent sampling was undertaken at that site (Table 1) and re-location tags were removed. The final trip was undertaken in April 2018 (post-austral summer) to Pandora and Orpheus to collect branches and reassess coral health and growth. Growth was assessed from photos of colony size calculated as change from April–Nov 2017 winter to Nov 2017–April 2018 summer. On the final collecting trip in April 2018, several corals at Pandora ($n = 7$) and Orpheus Island ($n = 12$) could not be re-located possibly due to loss of marking tags and/or the result of poor visibility from heavy

freshwater flooding events. All of those corals that could not be located, however, had a visual health score of 4 or greater in Nov 2017, which is a non-bleaching, heavily pigmented colour category and mortality was not assumed.

Coral bleaching and growth

Coral health and size (based on arithmetic mean radius and surface area) were assessed by digital analysis using ImageJ software. The images were taken from above making sure to frame the individual, and the coral health chart (Siebeck et al. 2006) used as a scale, to measure the different degrees of bleaching. The coral health chart provides a six-point scale: from 1 (severely bleached) to 6 (healthy coral with strong pigmentation) based on the brightness/saturation scale within four colour hues, to determine coral bleaching and changes in coloration (Fig. 1). To analyse coral health from the images taken in the field, mean grey-values were recorded for each scale grade on ImageJ and used to build a regression curve. Three points from random locations on the coral were then measured in visually similar light conditions,

i.e. not taken from shaded portions of the colony. These values were extrapolated to the regression curve to obtain health values ranging from 0 to 6 + (Cantin, unpublished).

To quantify growth parameters, each image was scaled and the outline of the coral traced to determine 2D planar surface area (SA; cm^2). In addition, the longest dimension of the coral was recorded. To measure arithmetic mean radius (AMR), as both of these species in general grow in a circular shape, SA was used to estimate the radius (SA $= \pi r^2$). The AMR produces a linear value (cm) to determine change in colony size as a proxy for growth through time.

Physiological analysis

Sampled branch fragments, ranging from 2 to 4 cm in length, were carefully removed from the tagged colonies, wrapped in aluminium foil with the corresponding tag number, and frozen for further analysis. Coral fragments were kept on ice during processing to reduce decomposition of the sample. The samples were individually placed in large ziplock bags, where they underwent tissue stripping (or tissue blasting). For each fragment, 7 ml of filtered seawater (0.22 μm) was added to the bag and the tissue was removed using a high-pressure airgun. This coral slurry was transferred into a 10-ml Falcon tube for subsequent subsampling. To ensure the collection of the remaining coral tissue, the process was repeated with 2 ml of water and then again with 1 ml. The coral slurry removed was homogenised for 30 s, and the final volume was recorded for posterior standardisation. The homogenised slurry was subsampled three times for chlorophyll a content analysis (1 ml); total protein content (1 ml); and zooxanthellae counts (1 ml), which was preserved with 10% formalin (200 μl). The remaining coral slurry was transferred to a 20 ml scintillation vial for posterior lipids analysis (Fig. S2). Detailed methods for determining chlorophyll a content, zooxanthellae density, protein and lipid content are available in Supplementary Materials.

Statistical Analysis

Linear mixed effects (lme) models were used to determine the significant difference between the fixed variables (visual health/growth/physiological parameters) and explanatory variables: coral taxa, location and sampling date with a nested effect of site (Table S1). Models that considered various explanatory variables were assessed using maximum likelihood (ML) and Akaike Information Criterion-corrected (AICc) to identify best-fit models. Model assumptions were validated with visual inspection of plotted residuals (linearity, homogeneity of variance, normality). Models with the lowest AICc were chosen; where two or more models returned the same AICc value, the simpler model was selected based on the rule of parsimony (Table S1). The selected model was then fit with REML to evaluate the statistics. Detailed statistical analysis and transformations for each of the lme can be found in Supplementary Materials.

The model averaging procedure applied here quantifies the magnitude of the regression coefficient for each variable in the presence and absence of all other variables (Burnham and Anderson 2002). Weighted AIC model averaging was used to assess the relative strength and direction of a variable in determining the visual health score and growth rates for each species, following Hoogenboom et al. (2011). For visual health score, the effect of physiological variables (lipid concentration, protein concentration, zooxanthellae density and chlorophyll a content) were modelled on visual health score to estimate the magnitude and strength of each of these predictor effects on coral visual health score for each species. For growth, the effects of colony longest diameter, visual health score, tissue quality and chlorophyll a were modelled to determine what predictor effects had the greatest strength for determining higher growth rates. Tissue quality is a combined variable of lipids and protein content standardised per unit SA, converted to energetic equivalents based on enthalpies of combustion (23.9 J mg^{-1} for protein and 39.5 J mg^{-1} for lipid, see Anthony and Fabricius 2000, Hoogenboom et al. 2011). First, each variable was standardised to have a mean of zero and a standard deviation of one, and then Akaike Information Criterion (AIC) was determined for each possible model (Table S2a,b,c,d). The Akaike weight (wAIC$_i$) for each model was calculated, and the wAIC$_i$ values were then summed over all models that contained that predictor variable to assess the support for a given predictor variable (wAIC$_j$). Lastly, model averaging was employed across regression parameters: each model's parameter estimate was weighted according to wAIC$_j$, which yielded the direction and magnitude of the effect of each variable. All statistical analyses were conducted in R (R Development Core Team 2020).

Results

Thermal stress on the central GBR

At our study sites in 2016, Pandora experienced the greatest thermal stress (maximum DHW ~ 4 °C-weeks), whereas Rib and Orpheus both experienced similar, but slightly lower values (~ 2–3 °C-weeks) (Fig. 2). The level of thermal stress at all three reefs was much higher in 2017; the highest thermal stress was experienced at Orpheus and Pandora (~ 8–9 °C-weeks), while at Rib it was slightly lower (~ 7 °C-weeks). While year-round SST values were well-correlated between all site pairs ($R^2 > 0.95$), when considering only extreme SST values that contributed to the thermal stress (DHW; i.e. SST $\geq$ MMM + 1 °C for both reefs),

Fig. 2 Sea surface temperature (SST) and thermal stress (as Degree Heating Weeks, DHW) for Rib, Orpheus and Pandora from Jan 1, 2015–May 1, 2018
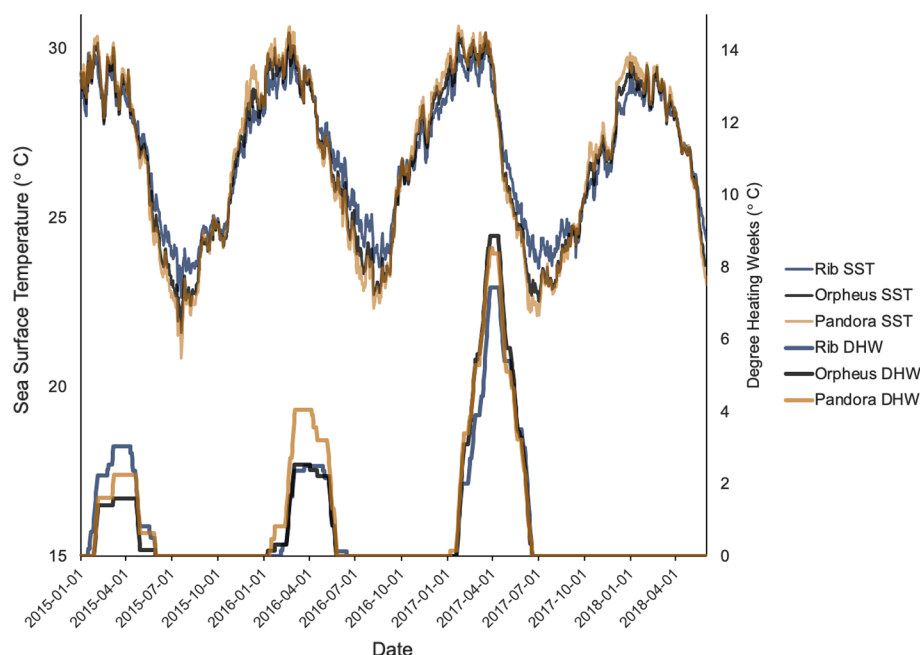
pair-wise comparisons indicated distinctions between the datasets (R^2 of 0.65 for Pandora-Orpheus, 0.13 for Pandora-Rib and 0.37 for Orpheus-Rib), showing thermal stress more similar between Pandora and Orpheus that was consistent with observed variations in thermal stress.

Mortality

A range of health scores were observed in April 2017 for both *A. millepora* and *P. acuta* (Fig. 3a, b). Four weeks after the first corals were surveyed (May 2017), a total of 9% (11/120) of corals had died (Fig. 3c, d). Of those 11 colonies that died, 9 had a bleaching health score of 2 or less with no visible signs of damage from COTS. The other two colonies were visibly healthy, pigmented and located at Rib Reef and therefore likely eaten by COTS. By Nov 2017, the highest rate of mortality was recorded with 78% (31/40) of corals dead at Rib Reef likely a result of the COTS outbreak as most had feeding scars and significant partial mortality, and there was still a high abundance of COTS in the area (Fig. 3e, f). As mentioned above, no subsequent collection was undertaken at Rib. A further 11% (9/80) of corals at Pandora and Orpheus died from bleaching by November 2017 and one colony of *P. acuta* at Orpheus could not be located. No further mortality was recorded from November 2017 to April 2018 of located colonies. Compared to Pandora, greater coral mortality was observed at Orpheus Island, with a reduction of 20% of *A. millepora* and 8% of *P. acuta* during the study (Fig. 3).

In April 2017, corals at Pandora and Orpheus with a health score of 3 or greater (fluorescing and/or darker pigmented colonies) had 100% survival during the study;
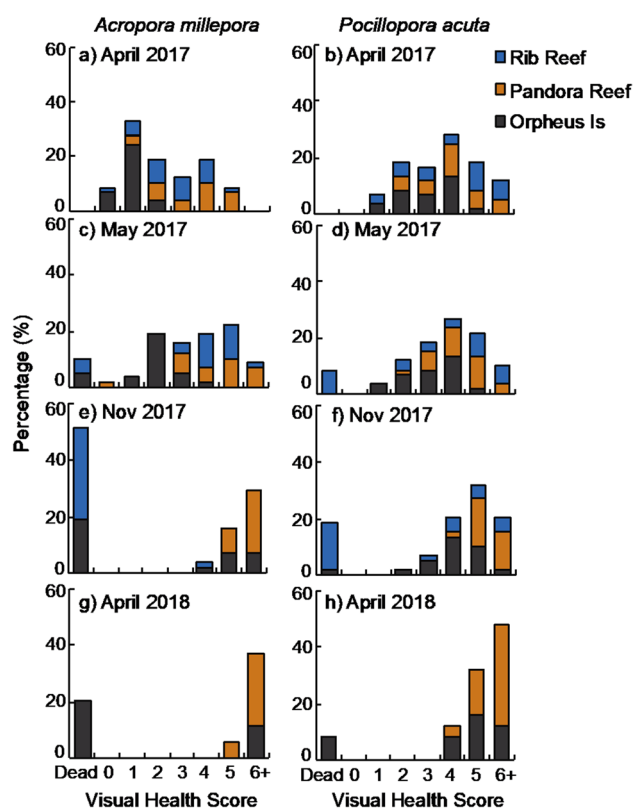

Fig. 3 Frequency distribution of visual health scores for *A. millepora* (aceg) and *P. acuta* (bdfh) at each sampling time point, April 2017 (**a**, **b**), May 2017 (**c**, **d**), Nov 2017 (**e**, **f**) and April 2018 (**g**, **h**). Visual health score ranges from 0 (fully bleached) to 6+ (healthy; see Fig. 1)
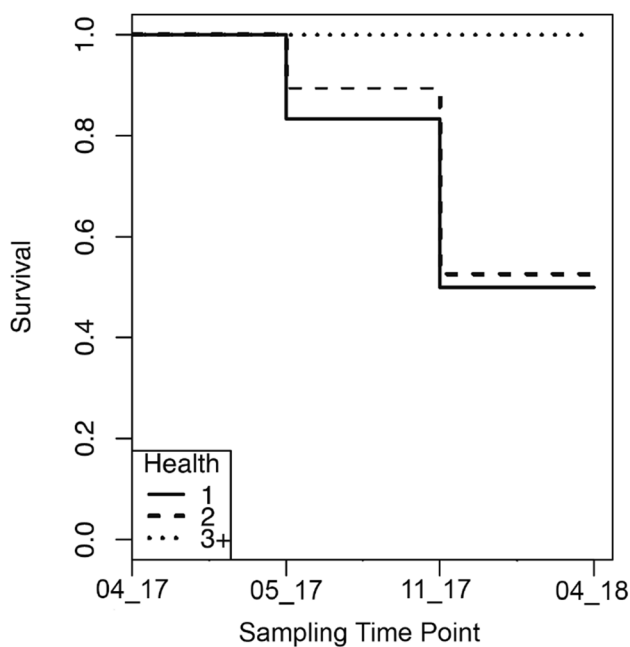
Fig. 4 Cox regression survival probability combined for both species at Pandora and Orpheus that had visual health scores 1, 2 and 3+ with initial sampling in April 2017 (04_17) and the following sampling time points: May 2017 (05_17), November 2017 (11_17) and April 2018 (04_18). Colonies at Rib were excluded from analysis

colonies at Rib were excluded from this consideration due to the confounding factor of COTS outbreak (Fig. 4). The difference in survival probability among health scores 1, 2 and 3 + was significant (Likelihood ratio test = 24.6 on 2 df, p = < 0.001). Repeated sampling of corals one month later in May 2017 showed a survival probability of 83% and 90% if they had a health score of 1 and 2, respectively, in April 2017. By November 2017, a further seven months

later, those corals that were heavily bleached in April 2017 (health scores 1 and 2) both had ~ 50% survival probability. Of our sampled colonies, no mortality was observed beyond the November 2017 time point meaning those that survived to that sampling date were still alive the following April 2018 (Fig. 4).

Corals at Orpheus Island were more prone to bleaching in April 2017 with the majority of *A. millepora* in the health score 2 and 3 category (Fig. 3a). The difference in bleaching health score between taxa was not significant; however, there was variation among locations with Orpheus having significantly lower bleaching health score compared to Pandora and Rib (lme p > 0.05, Fig. 5, Table S3). In April 2017 during peak heat stress, 100% of the *Acropora* corals at Orpheus Island had a health score < 3 compared to 30% of the *A. millepora* at Pandora. In general, corals at Pandora experienced lower bleaching severity and no mortality was recorded. The overall visual health of corals on the reef gradually improved through each successive sampling trip with no bleaching recorded for our 2 focal species in Nov 2017 and April 2018 (Fig. 3).

Growth

The model that best explained the growth data, by comparison of AICc, included season, location and genus as the explanatory variables with health and size not identified in the model (Table S1). The lack of inclusion of health in the model is likely due to the exclusion of dead corals (which thus did not exhibit growth). If corals were heavily bleached (visual health scores of 1 and 2), they likely succumbed to mortality and on subsequent sampling a growth rate could not be determined. Investigation of the models that included visual health as a predictor variable confirmed the visual

Fig. 5 Average coral visual health score for *P. acuta* and *A. millepora,* and each sampling location (Pandora, Orpheus, Rib), and by sampling date (April 2017, 04_17; May 2017, 05_17; Nov 2017, 11_17; April 2018, 04_18) during the study
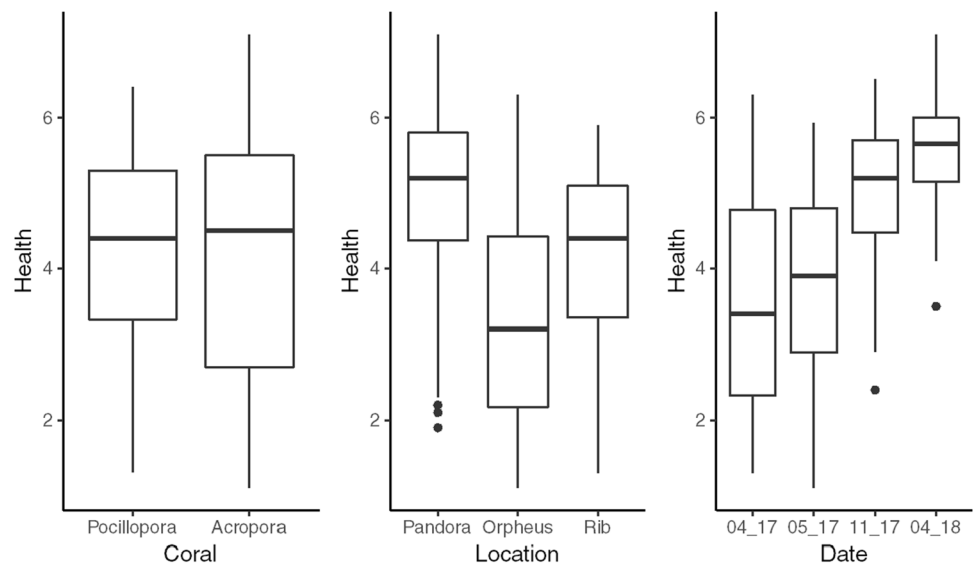
health score did not significantly impact growth determined by proportional change in area or ARM (lme $p > 0.05$).

When investigating growth rates by AMR, there was a significant difference between *A. millepora* and *P. acuta* (Table S4, Tukey post hoc test p-adj $= 0.001$) with average growth rates being at least two times greater for *A. millepora* (Fig. 6, Table S4). Growth rates were also significantly greater in summer (Nov'18–April'19) compared to winter (April–Nov'18) (Fig. 6, Table S4) where growth of *A. millepora* and *P. acuta* were 35–40% and 23–33% greater in the summer, respectively. Despite growth rates being in general greater at Pandora than Orpheus, the difference was non-significant (Table S4, Tukey's post hoc test p-adj $= 0.075$). *P. acuta* at Rib Reef, on average, experienced negative growth (considered as due to COTS predation) and that site was excluded from the model on growth (Fig. S3, Table S5).

Similar trends were observed when investigating growth based on proportional change in SA. *A. millepora* average growth rates were significantly greater (10–17%) than *P. acuta* based on proportional change in SA (Fig. 6, Table S5, Table S6). Seasonal growth rate differences were also significant (Fig. 6, Table S6) being 50% greater in summer for each species. In addition, there was a non-significant difference in proportional change in SA between Orpheus and Pandora (Table S6). All corals at Rib Reef except one *P. acuta* had negative growth [proportional change in SA < 1 (Fig. S3)].

Fig. 6 Growth rates of *A. millepora* (**a**, **c**) and *P. acuta* (**b**, **d**) based on arithmetic mean radius (cm 6-months^{-1}) (**a**, **b**) and proportional change in surface area (SA) standardised to 6-months (**c**, **d**) in winter (April-Nov 2017) and summer (Nov 2017-April 2018)
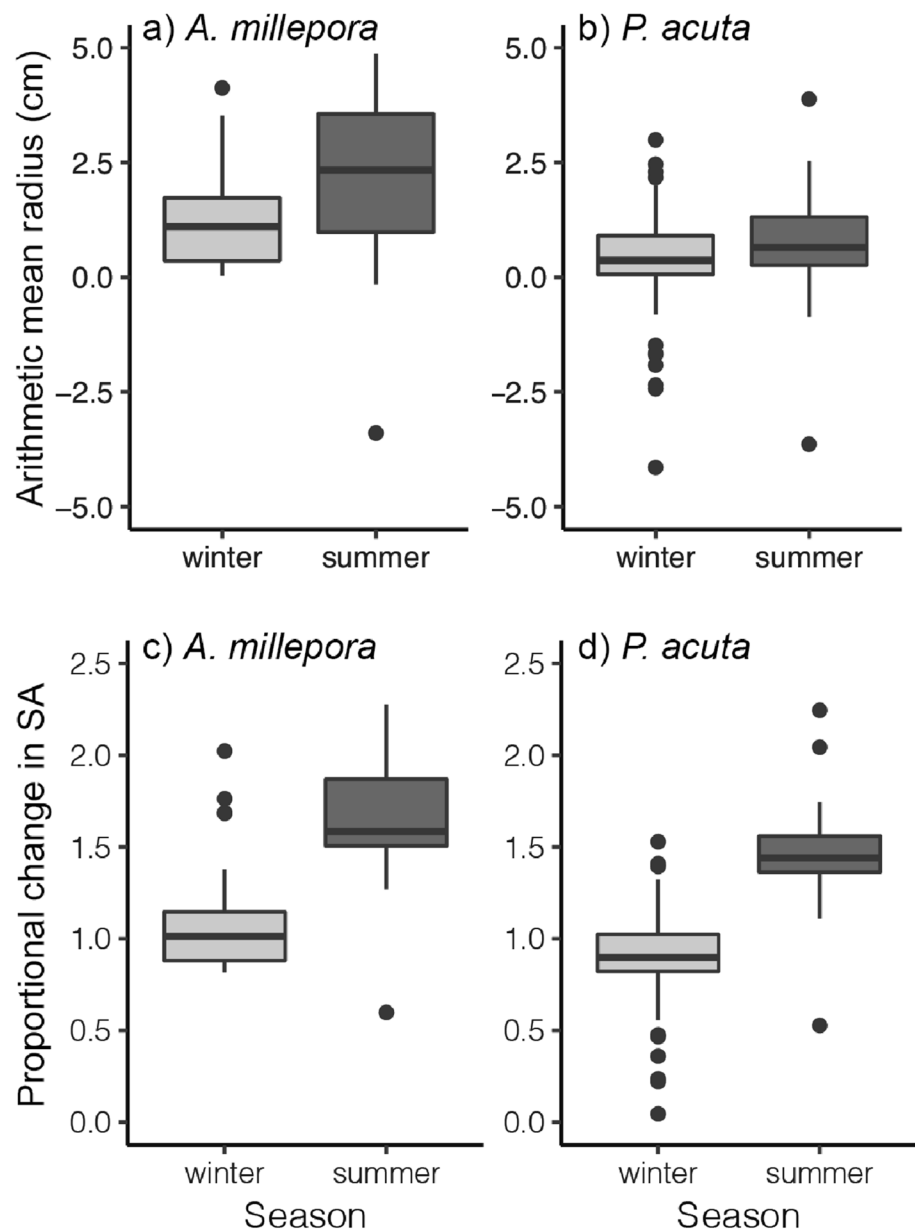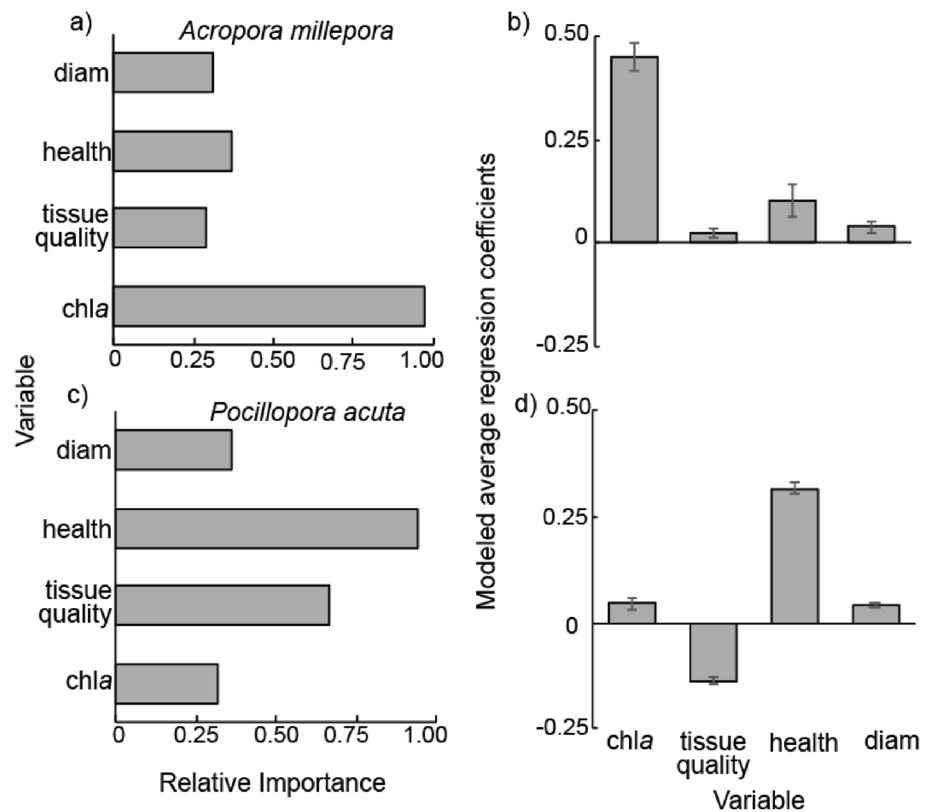
Fig. 7 The relative importance of diameter (diam), health score, tissue quality and chlorophyll *a* (chl*a*) concentration in determining growth rate for **a** *A. millepora* and **c** *P. acuta* and the associated modelled average regression coefficients for **b** *A. millepora* and **d** *P. acuta*

There was variability in the relative importance of response variables in determining growth for each species (Fig. 7). For *A. millepora*, chlorophyll *a* content was the strongest predictor of growth rates, whereas for *P. acuta* the health score was the most important variable. Higher values of chlorophyll *a*, tissue quality, health and colony diameter were all positively associated with greater growth rates for *A. millepora*. However, for *P. acuta*, tissue quality (the combined variable of lipid and protein content) displayed a negative correlation.

Coral physiology

The most parsimonious model for chlorophyll *a* content and zooxanthellae density had the additive factors of genus, location and visual health score. For lipids, the model with the lowest AICc included only genus or date as the random effects. However, from exploratory data analysis, there was some variability by sampling date. The interaction between genus and sampling date was excluded based on AICc, and the final model for lipid had the additive factor of date but excluded visual health score and genus. For protein, the model with the lowest AICc only included the sampling date, and the fixed effects of genus, location and health score were deemed not significant in explaining the model trends based on AICc.

Chlorophyll *a* content average values for *A. millepora* (8.1 ± 0.8 µg cm^{-2}, mean $\pm$ SE) were almost twice that of *P. acuta* (4.6 ± 0.4 µg cm^{-2}), a statistically significant variation (Fig. 8, Table S7). Chlorophyll *a* content increased throughout the year and was significantly greater in April 2018 than in May 2017 and Nov 2017 (Fig. 8c, d, Table S7), driven largely by *A. millepora*. Chlorophyll *a* content showed significant variation aligning as expected with the decreasing visual health score of each coral, with significantly less chlorophyll *a* at lower health scores (Fig. 8b, d, Table S7). For example, the average chlorophyll *a* content of corals with a health score of 1 was 2.1 ± 0.9 µg cm^{-2} and 1.2 ± 0.8 µg cm^{-2} for A. *millepora* and *P. acuta*, respectively, compared to health score 6 values of 12.6 ± 0.9 µg cm^{-2} and 5.4 ± 0.6 µg cm^{-2}, respectively. There was no relationship between chlorophyll *a* content and zooxanthellae density for either species (Fig. S4, $R^2 = 0.00$ for both). Average zooxanthellae density of *A. millepora* (6300 ± 500 cell cm^{-2}) was twice that of *P. acuta* (3200 ± 200 cell cm^{-2}). Zooxanthellae density significantly varied by location, with lower densities recorded at Rib reef than Orpheus and Pandora (Table S8). Zooxanthellae density followed an opposite temporal trend to chlorophyll *a* content with significantly lower densities in Nov 2017 (4000 ± 300 cell cm^{-2}) and April 2018 (4200 ± 500 cell cm^{-2}), compared to May 2017 (5400 ± 500 cell cm^{-2}) (Table S8).

Fig. 8 Chlorophyll *a* content (µg cm^{-2}), lipid content (mg cm^{-2}), and protein content (mg cm^{-2}) for *A. millepora* (**a, b, e, f, i, j**) and *P. acuta* (**c, d, g, h, k, l**) by sampling date (year_month, left panel) and visual health score (right panel)
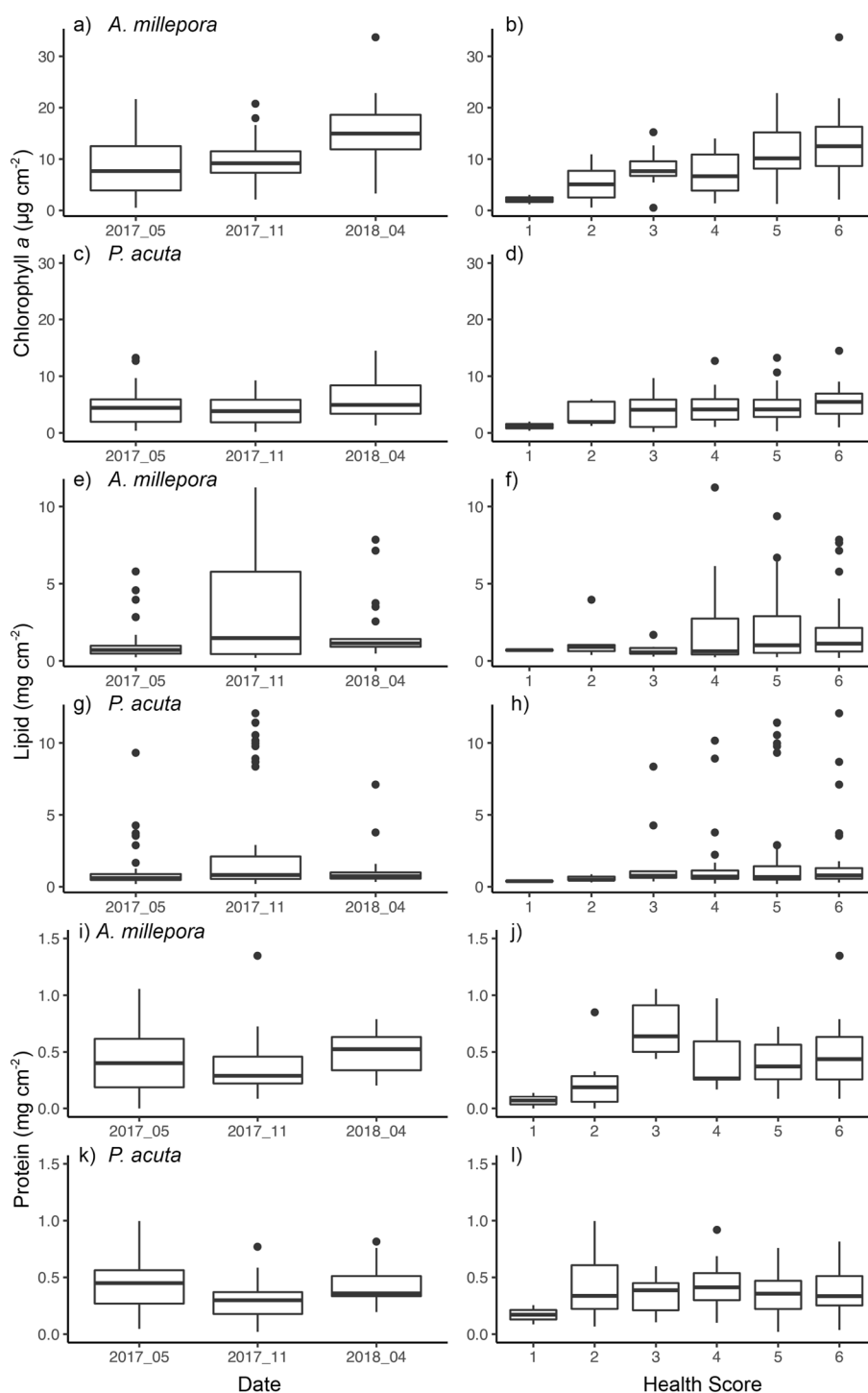
Lipid and protein concentrations were more varied among health score and sampling date and did not follow the same trend of increasing with health scores as with chlorophyll *a* content (Fig. 8). Lipid and protein concentrations were generally lower when they had a low health score but there was high variability. For example, *A. millepora* average protein was lowest in health score 1 (0.07 ± 0.1 mg cm^{-2}) and highest in health score 3 (0.46 ± 0.7 mg cm^{-2}) and *P. acuta* was lowest in health score 1 (0.17 ± 0.1 mg cm^{-2}) and highest in health score 2 (0.45 ± 0.4 mg cm^{-2}) (Fig. 8j, l). Lipid concentrations were similar among species (average values for both *A. millepora* and *P. acuta* were 1.8 ± 0.2 mg cm^{-2}) and significantly varied by sampling date (Table S9). Lowest lipid concentrations were found in May 2017 (1.1 ± 0.2 mg cm^{-2} for both species) compared to Nov 2017 (3.0 ± 0.7 mg cm^{-2}

and 2.6 ± 0.6 mg cm^{-2} for *A. millepora* and *P. acuta*, respectively) and April 2018 (1.9 ± 0.4 mg cm^{-2} and 1.2 ± 0.3 mg cm^{-2} for *A. millepora* and *P. acuta*, respectively). Similarly, protein concentrations were similar among *A. millepora* (0.43 ± 0.03 mg cm^{-2}) and *P. acuta* (0.37 ± 0.02 mg cm^{-2}) but displayed significant difference with sampling periods (Table S10). Protein concentrations were significantly lower in pre-summer (Nov 2017) than in either post-summer measurement for both species (0.38 ± 0.3 mg cm^{-2} and 0.29 ± 0.2 mg cm^{-2} for *A. millepora* and *P. acuta*, respectively, Fig. 8i, k). Based on model comparisons by AICc, there was no significant difference among reefs or health score in lipid and protein concentrations (Table S1).

The most strongly correlated predictor of *A. millepora* and *P. acuta* health scores was chlorophyll *a* (Fig. 9a, c), with health scores increasing with greater chlorophyll *a* content in both species. Modelled average regression coefficient values for chlorophyll *a* were significantly greater than zero for both species (Fig. 9b, d). The second greatest predictor was lipid content for both species and also displayed a positive directionality, indicating higher lipid content was correlated with higher health score. Zooxanthellae density and protein content were not significant in determining the health score for *A. millepora* (Fig. 9b). For *P. acuta*, however, they displayed a negative directionality

meaning higher abundances were associated with lower health scores (Fig. 9d).

Discussion

This study investigated the survivorship, growth and physiology of two species of corals (*A. millepora* and *P. acuta*) at three reefs on the central GBR at three time points: during peak heat stress in 2017 (April/May 2017), before the onset of the 2017/18 austral summer (November 2017), and after austral summer in April 2018. We were particularly interested in how survivorship and bleaching severity differed between locations and how growth and physiology changed in relation to coral visual health score. For example, does a coral with a higher health score possess more chlorophyll *a*, lipids and proteins and does this equate to a greater growth rate for those corals?

We found heterogeneity in bleaching severity and mortality among locations. Pandora suffered no coral mortality although a low proportion of corals (9/40; 23%) were visually scored at risk of bleaching by health category scale following peak heat stress in April 2017. A visual health score of 2 or less is indicative of severe bleaching and was associated with a 50% probability of survival (Fig. 5). The ranking of bleaching severity among our tagged corals in 2017 was Orpheus Island > Rib Reef > Pandora Reef.

Fig. 9 The relative importance of chlorophyll *a* (chl*a*) concentration, lipids, protein and zooxanthellae density (zoox) in determining the visual health score for **a** *A. millepora* and **c** *P. acuta* and the associated modelled average regression coefficients for **b** *A. millepora* and **d** *P. acuta*. Non-significant relationships denoted by 'n.s.'
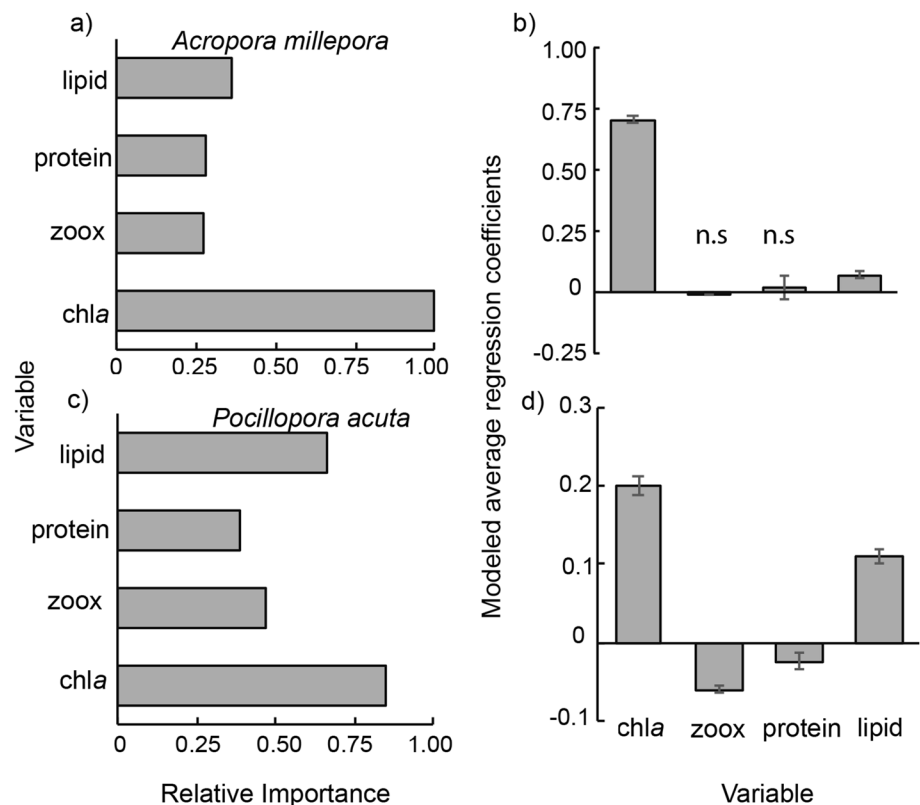
However, Rib Reef corals were tagged to match the depths at Pandora and Orpheus sites, and as a result, the crest was excluded where the majority of corals were heavily bleaching and fluorescing in April 2017 (pers. Obs). The bleaching severity did not match the observed DHW pattern (Orpheus ≳ Pandora > Rib) for the reefs during the 2017 heat stress event (Fig. 3). This disparity is likely due to the geographic locations of our study sites. Pandora and Orpheus reefs are both described as inshore reefs. However, Orpheus Island is found 13 km from the mainland and in general has better water quality than Pandora (Anthony 2000). Pandora is closer to shore, where land-based runoff of silt and nutrients are high (Done et al. 2007). These conditions have strongly influenced the coral community, which has been exposed to long-term and short-term disturbances such as flood plumes, cyclones and heat waves (Done et al. 2007).

The relationship between suspended sediments and thermal stress is complex but may be beneficial at low sediment loads (Fisher et al. 2019), such as Pandora. In decreased light availability, photosynthesis activity declines and corals may not meet their energetic requirements (Grottoli et al. 2006). Corals can adapt to heterotrophy, ingesting suspended particulate food, despite their low quality and nutritional value (Lehman 1976). This way corals can meet their energetic demands and increase their lipids reserve, reducing the risk of mortality (Anthony 2000). Anthony (2000) demonstrated that both species *A. millepora* and *P. damicornis* are capable of heterotrophic feeding in highly turbid conditions. This adaptation could explain the higher survival and visual health in both species of coral at Pandora.

Higher growth rates in the austral summer during this study are not surprising given that any bleached corals that survived through austral winter would have had to focus energy resources on repairing damage and likely did not have an excess of energy allocation for skeletal growth. This intra-annual variability in growth rates contrasts to previous studies (e.g. Anderson et al. 2017) that observed similar seasonal calcification rates of *P. damicornis* during a year with no bleaching on the central GBR, in 2013–14 summer and 2014-winter. As calcification rates have been shown to increase under elevated temperatures (Lough and Barnes 2000, Pratchett et al. 2015), this sublethal effect of slower growth during the summer months suggests summer temperatures may already have been approaching upper thermal limits in corals prior to the 2016–2017 bleaching events. *A. millepora* growth rates determined by AMR were on average 2× that of *P. acuta* in this study (Fig. 5). However, *Pocillopora* branches tend to be thicker and have higher density than Acroporids (Anderson et al. 2017). The methods for determining growth in this study do not capture the mass of skeletal deposition which may be a more similar metric of growth for these species. That is a limitation in this study when using surface area alone to measure growth,

but long-term studies on branching coral growth (such as Anderson et al. 2017) require sacrifice of the coral and therefore repeated physiological sampling and insight into those changes through time at a colony level cannot be completed.

When investigating the physiological variables that were contributing to coral growth, the major contributor for higher growth rates was chlorophyll *a* for *A. millepora* and visual health score for *P. acuta*. As visual health for *P. acuta* was highly correlated with chlorophyll *a* content, these findings suggest that the translocation of energy from the symbionts is the most important method for energy transfer for growth in both these corals. This result highlights the sublethal implications of bleaching and/or reductions in chlorophyll *a* content during heat stress. The majority of heavily bleached, physiologically compromised corals were excluded from the analysis of physiological properties that contribute to a greater growth because they died following the heat stress and a second sampling point was therefore not available to quantify growth. However, ~50% of corals with a visual health score of 1 and 2 survived (Fig. 5). Corals with a visual health score of 1 had 4.5 and 6 times less average chlorophyll *a* content than those with visual health score of 6 for *P. acuta* and *A. millepora*, respectively (Fig. 9). The presence of more thermotolerant Symbiodinium in coral populations may be the dominant factor in survival and growth of these fast-growing species as bleaching events, predicted to become increasingly recurrent, stress the reefs (Logan et al. 2014).

Physiological implications

The bleaching susceptibility and the health of corals are determined by a complex interaction of factors (Maina et al. 2008). They can be environmental factors such as temperature, light, water quality (Anthony et al. 2009) or biological factors like coral acclimation from prior exposure to heat stress (Ainsworth et al. 2016), zooxanthellae identity (Berkelmans and van Oppen 2006), physiological traits like thinner tissues (Loya et al. 2001), heterotrophic feeding capacity (Anthony et al. 2000; Grottoli et al. 2006), and regulation of their physiology (Gates and Edmunds 1999; Schoepf et al. 2013). For both species in this study, chlorophyll *a* content was the strongest variable contributing to visible health scores, followed by lipids. As corals with a visual health score of 3 and greater had a 100% probability of survival, this study supports previous findings (Grottoli et al. 2006; Schoepf et al. 2013) illustrating that of the variables tested here, chlorophyll *a* and lipids were the strongest predictors in determining a corals survival.

During coral bleaching, corals are energy deficient due to the loss of the mutualist relationship with their symbiotic zooxanthellae. As a result, they convert to drawing upon their own lipid supply (Rodrigues and Grottoli 2007).

Therefore, we hypothesised that a decrease in visual health score may lead to a lower abundance of lipids. Unsurprisingly, lipids were the second most important predictor of health score demonstrating that more-pigmented corals often have a higher abundance of lipids. Zooxanthellae density was also assumed to be more important in coral health as the coral health card colours reflect changes in zooxanthellae density and chlorophyll *a* content but only when the colour was determined to be at least two units apart (Siebeck et al. 2006). However, in weighted-modelled averaging, strong multicollinearity such as that observed between chlorophyll *a* content and zooxanthellae density can result in model-averaged regression coefficients being not significantly different from zero for explanatory variables when they do not have independent effects on the response variable (Hoogenboom et al. 2011). This likely explains the non-significant result in *A. millepora* as chlorophyll *a* was the most important response variable (Fig. 9b) and zooxanthellae density was not significantly different to zero. Conversely, zooxanthellae density was negatively associated with visual health score in *P. acuta* suggesting this species is more resistant to thermal stress as corals with a lower visual health score are able to retain their zooxanthellae. Alternatively, these corals were harbouring thermotolerant zooxanthellae allowing retention during a thermal stress event.

Chlorophyll a and zooxanthellae

Chlorophyll *a* content significantly increased simultaneously with the visual health score (Fig. 9, Table S7). In May 2017, the chlorophyll *a* content was the lowest; these findings are in accordance with previous bleaching studies where thermal stress led to declines in chlorophyll *a* content (Fitt et al. 2000; Grottoli et al. 2004). An increase in abundance was observed following the heat stress and in April 2018 the chlorophyll *a* content was significantly higher than the initial sampling point. Chlorophyll *a* concentration in corals has also been observed to follow seasonal patterns (Fitt et al. 2000). The high sea surface temperatures encountered in the summer affect the zooxanthellae by causing irreversible damage in the photosystem II, known as "chronic" photoinhibition (Warner et al 1999; Fitt et al. 2000). The carbon fixation is reduced during period of high light due to a reversible down-regulation of the photosynthesis. This process is called dynamic photo regulation (Fitt et al. 2000). It occurs in Indo-pacific corals, where cycling of specific carotenoids avoids directing harmful protons towards the reaction centres, lowering the chlorophyll *a* content during the brightest point of the day (Brown et al. 1999). These two regulation mechanisms could be applied during bleaching periods, which could explain the lower chlorophyll *a* content in the summer, and the increase during the winter.

Conversely, zooxanthellae density significantly differed between sampling times and had the lowest densities after the austral summer in April 2018 (Table S8). Rodrigues and Grottoli (\2007) hypothesised that increasing chlorophyll *a* per cell might be more efficient for the whole organism than to regrow new zooxanthellae. The differences in zooxanthellae density in our study may also reflect the variability in bleaching severity among our corals as visual health score did not show significant variation in zooxanthellae density either (Table S8). Other studies have shown seasonal trends of lowest densities of zooxanthellae density in late summer/early fall, peak levels in the winter and/or spring, decreasing again during the next summer similar to this study (Fitt et al. 2000). Alternatively, the coral ability to acclimatise to thermal stress could explain the variation in symbiont density throughout the year. These corals survived the 2016 heat stress event and during that time, there may have been a shift in endosymbionts towards the thermotolerant clades. The shift of clades has been demonstrated for *A. millepora*, where the symbionts genotype strongly influenced coral fitness, and the survival and thermal tolerance (Berkelmans and van Oppen 2006). The shift in endosymbionts was also confirmed in *P. damicornis* by Rowan (2004). Further analysis of the microbial community is advised to confirm whether the individuals in this study present the more-thermally resistant clades, a greater abundance of which would explain the temporal pattern observed here.

Proteins

The average protein content found for both species was higher following the bleaching event and then decreased to November 2017 and April 2018. The increase in transcription of proteins could be explained by the up-regulation of heat-shock proteins (hsps) under high temperature stress (Gates and Edmunds 1999; Rosic et al. 2011; Hoadley et al. 2015). Hsps function as molecular chaperones, having a crucial role in folding, unfolding, aggregation, degradation, and transport preventing further damage of the proteins (Coles and Brown 2003). The transcription of these proteins has been demonstrated for *A. millepora* and *P. damicornis* (Hoadley et al. 2015). The regulation of the enzyme activity could also be a response to thermal stress. *P. damicornis* have shown increased activity of antioxidant enzymes, superoxide dismutase (SOD) and catalase (CAT) as a response to elevated temperature and UV radiation (Lesser et al. 1994). The rates of protein turnover are directly related to the coral's ability to acclimatise (Gates and Edmunds 1999).

Lipids

The energy state of an organism is a function of the current and past energy intakes and losses, growth rate, energy allocation and the physiological performance, all of which have implications for survival and fitness (Maltby 1999). In corals, the zooxanthellae provide the host with ~ 90% of the daily metabolic energy requirements due to their photosynthetic capacity (Grottoli et al. 2006). When all the energetic demands are met and an excess of carbon is produced, the excess is stored in the host as lipids (Anthony et al. 2009). During a bleaching period, the number of zooxanthellae decreases; thus, the coral cannot meet its energetic requirements (Fitt et al. 2000). At this point, the organisms can draw upon lipid reserves as an energy source (Grottoli et al. 2006; Schoepf et al. 2013). The energy dynamics and the availability of lipids have an influence on the coral's capacity to survive thermal stress (Anthony et al. 2009).

The lipid content of *A. millepora* and *P. acuta* in this study was lower during the early-2017 bleaching event and increased during the winter, coincident with improved coral visual health. In November 2017, the lipid content was the highest but by April 2018 had decreased again. In the summer and autumn months, seasonally high water temperature increases respiratory rates and, thus, corals require more energy, which cannot be attained only by photosynthesis; as a consequence, lipid reserves are used (Fitt et al. 2000; Grottoli et al. 2004). In the winter and spring months, the energetic demands are lower leading to an excess production of carbon and new lipid synthesis and storage, increasing the average content.

Multiple disturbances

Rib Reef was impacted by multiple disturbances during this study; a crown-of-thorns starfish outbreak and thermal stress. Six months after the corals were tagged at Rib Reef in November 2017, 95% of *A. millepora* and 50% of *P. acuta* had died. Of the 11 individuals who survived until Nov 2017, 90% had negative growth based on proportional change in SA (Fig. S2) with some having 95% colony mortality. Based on presence of COTS (density, on average, 6.3 starfish per 100 m^2 ± 1.1 SE) (Burn et al. 2020), and the presence of feeding scars on the tagged colonies, it is highly likely that COTS grazing greatly contributed to the full and partial mortality experienced at Rib Reef, either through direct feeding or additive stress.

Acute disturbances, such as the passing of a cyclone and COTS outbreaks, contributed more to mortality of corals on the GBR (1.62 and 1.42% yr^{-1}, respectively) than bleaching (0.34% yr^{-1}) for the period 1985–2012 (De'ath et al. 2012). Recent data suggest ~ 40% decline in coral cover over the last 30 years on the GBR has been attributed to COTS outbreaks (Mellin et al. 2019). However, the chronic effects of bleaching-level heat stress is likely to be a major contributor to coral decline, with an estimated 30% reduction in shallow-water coral cover due to the 2016 bleaching event on the GBR (Hughes et al. 2017). A further 20% reduction was estimated due to the 2017 event (Hughes et al. 2019). Coral cover in the central GBR declined from 22% in 2016 to 12% in 2019, mainly attributed to back-to-back bleaching, COTS outbreak and tropical cyclone Debbie (AIMS LTMP, 2021). Managing the cumulative impacts of stressors on the reef is the greatest challenge for governance. Ultimately, predicted increases in the severity and frequency of future coral bleaching events is the greatest threat to sustaining the long-term function of coral reefs (Logan et al. 2014).

Conclusion

This study demonstrates how the bleaching event of 2017 impacted the visual health and physiology of *A. millepora* and *P. acuta.* Visibly bleached corals in the most-severe categories (health score of 1 and 2) had 50% chance of survival, but those with less-severe or no bleaching (health score 3 +) all survived. The corals at Pandora were less-severely impacted by heat stress than at Orpheus, which suggests that location disturbance history is an essential factor in determining coral sensitivity to bleaching. Chlorophyll *a* and lipid concentration were the most important of the factors measured in determining both growth rates and visual health score. Overall, the recovery and resilience of corals depends on a complex interaction of abiotic and biotic factors. The shift to more-thermally resistant *Symbiodiniaceae* likely plays a key role in coral resilience (Berkelmans and van Oppen 2006; Fuller et al 2020). Nonetheless, the host also plays an important role by the transcription of heat-shock proteins, antioxidant enzymes (Gates and Edmunds 1999), the use of lipids reserves (Anthony et al. 2009) and heterotrophy (Anthony 1999). The combination of these factors is important for corals to become more resilient and potentially withstand future bleaching events. Moreover, as this study highlights the important role the *Symbiodiniaceae* and chlorophyll *a* play in growth and survival, continued research such as (van Oppen et al. 2015) to enhance the local population of thermotolerant *Symbiodiniaceae* may provide the best chance of maintaining coral reef function in relation to the presence of fast-growing branching species.

Declarations

References

AIMS (Australian Institute of Marine Science) (2021) Long-term Reef Monitoring Program- Annual Summary Report on Coral Reef Condition for 2019/20. https://www.aims.gov.au/reef-monitoring/gbr-condition-summary-2019-2020. Accessed 23/3/2021

Ainsworth TD, Heron SF, Ortiz JC, Mumby PJ, Grech A, Ogawa D, Eakin CM, Leggat W (2016) Climate change disables coral bleaching protection on the Great Barrier Reef. Science 352:338–342

Anderson KD, Cantin NE, Heron SF, Pisapia C, Pratchett MS (2017) Variation in growth rates of branching corals along Australia's Great Barrier Reef. Scientific Reports 7:2920

Anthony K (2000) Enhanced particle-feeding capacity of corals on turbid reefs (Great Barrier Reef, Australia). Coral Reefs 19:59–67

Anthony KRN, Fabricius KE (2000) Shifting roles of heterotrophy and autotrophy in coral energetics under varying turbidity. Journal of Experimental Marine Biology and Ecology 252:221–253

Anthony KRN, Connolly SR, Hoegh-Guldberg O (2007) Bleaching, Energetics, and Coral Mortality Risk: Effects of Temperature, Light, and Sediment Regime. Limnology and Oceanography 52:716–726

Anthony KRN, Hoogenboom MO, Maynard JA, Grottoli AG, Middlebrook R (2009) Energetics approach to predicting mortality risk from environmental stress: a case study of coral bleaching. Functional Ecology 23:539–550

Baird AH, Bhagooli R, Ralph PJ, Takahashi S (2009) Coral bleaching: the role of the host. Trends in Ecology & Evolution 24:16–20

Bahr KD, Tran T, Jury CP, Toonen RJ (2020) Abundance, size, and survival of recruits of the reef coral Pocillopora acuta under ocean warming and acidification. PLoS ONE 15(2):e0228168. https://doi.org/10.1371/journal.pone.0228168

Baum JK, Claar DC, Tietjun KL, Magel JM, Maucieri DG, Cobb KM, McDevitt-Irwin JM (2023) Transformation of coral communities subjected to an unprecedented heatwave is modulated by local disturbance. Science Advances 9:eabq5615. https://doi.org/10.1126/sciadv.abq5615

Berkelmans R, van Oppen MJH (2006) The role of zooxanthellae in the thermal tolerance of corals: a "nugget of hope" for coral reefs in an era of climate change. Proceedings of the Royal Society B-Biological Sciences 273:2305–2312

Brown BE, Dunne RP, Ambarsari I, Le Tissier MDA, Satapoomin U (1999) Seasonal fluctuations in environmental factors and variations in symbiotic algae and chlorophyll pigments in four Indo-Pacific coral species. Marine Ecology Progress Series 191:53–69

Burnham KP, Anderson DR (2002) Model selection and inference: a practical information theoretic approach, 2nd edn. Springer-Verlag, New York, NY

Burn D, Matthews S, Caballes CF, Chandler JF, Pratchett MS (2020) Biogeographical variation in diurnal behaviour of Acanthaster planci versus Acanthaster cf. solaris. PLos one 15:e0228796

Cesar H, Burke L, Pet-Soede L (2003) The economics of worldwide coral reef degradation. International Coral Reef Action Network

Claar DC, Starko S, Tietjen KL et al. (2020) Dynamic symbioses reveal pathways to coral survival through prolonged heatwaves. National Community 11:6097 (2020). https://doi.org/10.1038/s41467-020-19169-y

Coles SL, Brown BE (2003) Coral bleaching - Capacity for acclimatization and adaptation. Advances in Marine Biology 46(46):183–223

Cooper TF, Berkelmans R, Ulstrup KE, Weeks S, Radford B, Jones AM, Doyle J, Canto M, O'Leary RA, van Oppen MJH (2011) Environmental Factors Controlling the Distribution of Symbiodinium Harboured by the Coral *Acropora millepora* on the Great Barrier Reef. Plos One 6

Darling ES, Timothy RM, Côté IM (2013) Life histories predict coral community disassembly under multiple stressors. Global Change Biology 19:1930–1940

De'ath G, Fabricius KE, Sweatman H, Puotinen M (2012) The 27–year decline of coral cover on the Great Barrier Reef and its causes. Proceedings of the National Academy of Sciences 109:17995–17999

Done T, Turak E, Wakeford M, DeVantier L, McDonald A, Fisk D (2007) Decadal changes in turbid-water coral communities at Pandora Reef: loss of resilience or too soon to tell? Coral Reefs 26:789–805

Dunn JG, Sammarco PW, LaFleur G Jr (2012) Effects of phosphate on growth and skeletal density in the scleractinian coral *Acropora muricata*: A controlled experimental approach. Journal of Experimental Marine Biology and Ecology 411:34–44

Fabricius KE, Logan M, Weeks S, Brodie J (2014) The effects of river run-off on water clarity across the central Great Barrier Reef. Marine Pollution Bulletin 84:191–200

Fisher R, Bessell-Browne P, Jones R (2019) Synergistic and antagonistic impacts of suspended sediments and thermal stress on corals. National Commun 10: 2346 https://doi.org/10.1038/s41467-019-10288-9

Fitt WK, McFarland FK, Warner ME, Chilcoat GC (2000) Seasonal patterns of tissue biomass and densities of symbiotic

dinoflagellates in reef corals and relation to coral bleaching. Limnology and Oceanography 45:677–685

Fuller ZL, Mocellin VJL, Morris LA, Cantin N, Shepherd J, Sarre L, Peng J, Liao Y, Pickrell J, Andolfatto P, Matz M, Bay LK, Przeworski M (2020) Population genetics of the coral Acropora millepora: Toward genomic prediction of bleaching. Science 369:eaba4674. https://doi.org/10.1126/science.aba4674

Gates RD, Edmunds PJ (1999) The Physiological Mechanisms of Acclimatization in Tropical Reef Corals1. American Zoologist 39:30–43

Glynn PW (1993) Coral reef bleaching: ecological perspectives. Coral Reefs 12:1–17

Great Barrier Reef Marine Park Authority, Australian Institute of Marine Science, and CSIRO (2022) Reef snapshot: Summer 2021–22, Great Barrier Reef Marine Park Authority, Townsville

Grottoli AG, Rodrigues LJ, Juarez C (2004) Lipids and stable carbon isotopes in two species of Hawaiian corals, Porites compressa and Montipora verrucosa, following a bleaching event. Marine Biology 145:621–631

Grottoli AG, Rodrigues LJ, Palardy JE (2006) Heterotrophic plasticity and resilience in bleached corals. Nature 440:1186–1189

Grottoli AG, Warner ME, Levas SJ, Aschaffenburg MD, Schoepf V, McGinley M, Baumann J, Matsui Y (2014) The cumulative impact of annual coral bleaching can turn some coral species winners into losers. Glob Change Biology 20:3823–3833. https://doi.org/10.1111/gcb.12658

Grottoli AG, Dalcin Martins P, Wilkins MJ, Johnston MD, Warner ME, Cai W-J, Melman TF, Hoadley KD, Pettay DT, Levas S, Schoepf V (2018) Coral physiology and microbiome dynamics under combined warming and ocean acidification. PLOS ONE 13:e0191156

Guest JR, Baird AH, Maynard JA, Muttaqin E, Edwards AJ, Campbell SJ, Yewdall K, Affendi YA, Chou LM (2012) Contrasting patterns of coral bleaching susceptibility in 2010 suggest an adaptive response to thermal stress. PLoS ONE 7:e33353

Heron SF, Maynard J, van Hooidonk R, Eakin CM (2016) Warming Trends and Bleaching Stress of the World's Coral Reefs 1985–2012. Scientific Reports 6:38402

Heron SF, Liu G, Eakin CM, Skirving WJ, Muller-Karger FE, Vega-Rodriguez M, De La Cour JL, Burgess TFR, Strong AE, Geiger EF, Guild LS, Lynds S (2014) Climatology development for NOAA Coral Reef Watch's 5-km product suite. NOAA Technical Report NESDIS 145. NOAA/NESDIS. College Park, MD. 30pp. https://doi.org/10.7289/V59C6VBS

Hoadley KD, Pettay DT, Grottoli AG, Cai W-J, Melman TF, Schoepf V, Hu X, Li Q, Xu H, Wang Y, Matsui Y, Baumann JH, Warner ME (2015) Physiological response to elevated temperature and pCO2 varies across four Pacific coral species: Understanding the unique host+symbiont response. Scientific Reports 5:18371

Hoegh-Guldberg O (2011) The impact of climate change on coral reef ecosystems. *Coral reefs: an ecosystem in transition*, 391–403

Hoogenboom MO, Connolly SR, Anthony KRN (2011) Biotic and abiotic correlates of tissue quality for common scleractinian corals. Marine Ecology Progress Series 438:119–128

Hughes TP, Kerry JT, Álvarez-Noriega M, Álvarez-Romero JG, Anderson KD, Baird AH, Babcock RC, Beger M, Bellwood DR, Berkelmans R, Bridge TC, Butler IR, Byrne M, Cantin NE, Comeau S, Connolly SR, Cumming GS, Dalton SJ, Diaz-Pulido G, Eakin CM, Figueira WF, Gilmour JP, Harrison HB, Heron SF, Hoey AS, Hobbs J-PA, Hoogenboom MO, Kennedy EV, Kuo C-y, Lough JM, Lowe RJ, Liu G, McCulloch MT, Malcolm HA, McWilliam MJ, Pandolfi JM, Pears RJ, Pratchett MS, Schoepf V, Simpson T, Skirving WJ, Sommer B, Torda G, Wachenfeld DR, Willis BL, Wilson SK (2017) Global warming and recurrent mass bleaching of corals. Nature 543:373

Hughes TP, Anderson KD, Connolly SR, Heron SF, Kerry JT, Lough JM, Baird AH, Baum JK, Berumen ML, Bridge TC, Claar DC, Eakin CM, Gilmour JP, Graham NAJ, Harrison H, Hobbs J-PA, Hoey AS, Hoogenboom M, Lowe RJ, McCulloch MT, Pandolfi JM, Pratchett M, Schoepf V, Torda G, Wilson SK (2018) Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. Science 359:80–83

Hughes TP, Kerry JT, Connolly SR, Baird AH, Eakin CM, Heron SF, Hoey AS, Hoogenboom MO, Jacobson M, Liu G, Pratchett MS, Skirving W, Torda G (2019) Ecological memory modifies the cumulative impact of recurrent climate extremes. Nat Clim Chang 9:40–43

Jones AM, Berkelmans R, van Oppen MJH, Mieog JC, Sinclair W (2008) A community change in the algal endosymbionts of a scleractinian coral following a natural bleaching event: field evidence of acclimatization. Proceedings of the Royal Society b: Biological Sciences 275:1359–1365

Jones A, Berkelmans R (2010) Potential costs of acclimatization to a warmer climate: Growth of a reef coral with heat tolerant vs. sensitive symbiont types. PLoS ONE 5(5): e10437. https://doi.org/10.1371/journal.pone.0010437

Kemp DW, Hernandez-Pech X, Iglesias-Prieto R, Fitt WK, Schmidt GW (2014) Community dynamics and physiology of Symbiodinium spp. before, during, and after a coral bleaching event. Limnology and Oceanography 59:788–797

LaJeunesse TC, Parkinson JE, Gabrielson PW, Jeong HJ, Reimer JD, Voolstra CR, Santos SR (2018) Systematic revision of Symbiodiniaceae highlights the antiquity and diversity of coral endosymbionts. Current Biology 28:2570–2580

Lehman JT (1976) The filter-feeder as an optimal forager, and the predicted shapes of feeding curves. Limnology and Oceanography 21:501–516

Lesser MP, Weis VM, Patterson MR, Jokiel PL (1994) Effects of morphology and water motion on carbon delivery and productivity in the reef coral, *Pocillopora damicornis* (Linnaeus): Diffusion barriers, inorganic carbon limitation, and biochemical plasticity. Journal of Experimental Marine Biology and Ecology 178:153–179

Liu G, Heron SF, Eakin CM, Muller-Karger FE, Vega-Rodriguez M, Guild LS, Rauenzahn JL, Geiger EF, Skirving WJ, Burgess TFR, Strong AE, Harris A, Maturi E, Ignatov A, Sapper J, Li J, Lynds S (2014) Reef-scale Thermal Stress Monitoring of Coral Ecosystems: New 5-km Global Products from NOAA Coral Reef Watch. Remote Sensing 6:11579–11606

Logan CA, Dunne JP, Eakin CM, Donner SD (2014) Incorporating adaptive responses into future projections of coral bleaching. Global Change Biology 20:125–139

Lough JM, Barnes DJ (2000) Environmental controls on growth of the massive coral Porites. Journal of Experimental Marine Biology and Ecology 245:225–243

Lough JM, Anderson KD, Hughes TP (2018) Increasing thermal stress for tropical coral reefs: 1871–2017. Scientific Reports 8:6079

Loya Y, Sakai K, Yamazato K, Nakano Y, Sambali H, Van WR (2001) Coral bleaching: the winners and the losers. Ecology Letters 4:122–131

Maina J, Venus V, McClanahan TR, Ateweberhan M (2008) Modelling susceptibility of coral reefs to environmental stress using remote sensing data and GIS models. Ecological Modelling 212:180–199

Maltby L (1999) Studying Stress: The importance of organism-level responses. Ecological Applications 9:431–440

Maynard JA, Anthony KRN, Marshall PA, Masiri I (2008) Major bleaching events can lead to increased thermal tolerance in corals. Marine Biology 155:173–182

Mellin C, Matthews S, Anthony KR, Brown SC, Caley MJ, Johns KA, Osborne K, Puotinen M, Thompson A, Wolff NH (2019) Spatial resilience of the Great Barrier Reef under cumulative disturbance impacts. Global change biology 25:2431–2445

Muller-Parker G, D'Elia CF, Cook CB (2015) Interactions between corals and their symbiotic algae. In: Birkeland C (ed) Coral Reefs in the Anthropocene. Springer, Dordrecht, pp 99–116

Pratchett MS, Anderson KD, Hoogenboom MO, Widman E, Baird AH, Pandolfi JM, Edmunds PJ, Lough JM (2015) Spatial, temporal and taxonomic variation in coral growth—implications for the structure and function of coral reef ecosystems. Oceanography and Marine Biology: An Annual Review 53:215–295

Rodrigues LJ, Grottoli A (2007) Energy reserves and metabolism as indicators of coral recovery from bleaching. Limnology and Oceanography 52. https://doi.org/10.4319/lo.2007.52.5.1874

Rosic NN, Pernice M, Dove S, Dunn S, Hoegh-Guldberg O (2011) Gene expression profiles of cytosolic heat shock proteins Hsp70 and Hsp90 from symbiotic dinoflagellates in response to thermal stress: possible implications for coral bleaching. Cell Stress and Chaperones 16:69–80

Rowan R (2004) Thermal adaptation in reef coral symbionts. Nature 430:742–742

Schoepf V, Grottoli AG, Warner ME, Cai W-J, Melman TF, Hoadley KD, Pettay DT, Hu X, Li Q, Xu H (2013) Coral energy reserves and calcification in a high-CO_2 world at two temperatures. PLoS one 8:e75049

Siebeck U, Marshall N, Klüter A, Hoegh-Guldberg O (2006) Monitoring coral bleaching using a colour reference card. Coral Reefs 25:453–460

Skirving WJ, Heron SF, Marsh BL, Liu G, De La Cour JL, Geiger EF, Eakin CM (2019) The relentless march of mass coral bleaching: a global perspective of changing heat stress. Coral Reefs 38:547–557

Skirving W, Marsh B, De La Cour J, Liu G, Harris A, Maturi E, Geiger E, Eakin CM (2020) CoralTemp and the Coral Reef Watch Coral Bleaching Heat Stress Product Suite Version 3.1. Remote Sensing 12:3856

Smith LD, Gilmour JP, Heyward AJ (2008) Resilience of coral communities on an isolated system of reefs following catastrophic mass-bleaching. Coral Reefs 27:197–205

van Oppen MJH, Oliver JK, Putnam HM, Gates RD (2015) Building coral reef resilience through assisted evolution. Proceedings of the National Academy of Sciences of the United States of America 112:307–2313

Warner ME, Fitt WK, Schmidt GW (1999) Damage to photosystem II in symbiotic dinoflagellates: A determinant of coral bleaching. Proceedings of the National Academy of Sciences 96:8007–8012