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Intraspecific Variation in Physiological Condition of Reef-Building Corals Associated with Differential Levels of Chronic Disturbance

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Abstract

Even in the absence of major disturbances (e.g., cyclones, bleaching), corals are subject to high levels of partial or whole-colony mortality, often caused by chronic and small-scale disturbances. Depending on levels of background mortality, these chronic disturbances may undermine individual fitness and have significant consequences on the ability of colonies to withstand subsequent acute disturbances or environmental change. This study quantified intraspecific variations in physiological condition (measured based on total lipid content and zooxanthellae density) through time in adult colonies of two common and widespread coral species (*Acropora spathulata* and *Pocillopora damicornis*), subject to different levels of biological and physical disturbances along the most disturbed reef habitat, the crest. Marked intraspecific variation in the physiological condition of *A. spathulata* was clearly linked to differences in local disturbance regimes and habitat. Specifically, zooxanthellae density decreased ($r^2 = 26$, df = 5,42, $p < 0.02$, B = -121255, p = 0.03) and total lipid content increased ($r^2 = 14$, df = 5,42, p = 0.01, B = 0.9, p = 0.01) with increasing distance from exposed crests. Moreover, zooxanthellae density was strongly and negatively correlated with the individual level of partial mortality ($r^2 = 26$, df = 5,42, $p < 0.02$, B = -7386077, p = 0.01). Conversely, *P. damicornis* exhibited very limited intraspecific variation in physiological condition, despite marked differences in levels of partial mortality. This is the first study to relate intraspecific variation in the condition of corals to localized differences in chronic disturbance regimes. The next step is to ascertain whether these differences have further ramifications for susceptibility to periodic acute disturbances, such as climate-induced coral bleaching.

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Introduction

Coral reefs are very dynamic ecosystems, impacted by a variety of natural and anthropogenic processes, which may vary in scale, frequency, and intensity [1]. Even in the absence of major disturbances (e.g., cyclones, bleaching or outbreaks of crown-of-thorns starfish), corals are still subject to a range of chronic, often small-scale disturbances that cause relatively high rates of background mortality (annual background mortality rates can generally vary from 1 to 30%: [2–5]). These background mortality agents (such as predation, competition and disease) are a normal part of the natural dynamics and turnover in coral populations and communities [6–8]. However, increases in prevalence and impact of chronic disturbances undermine the resilience of coral colonies and populations [4,5,8,9,10], which are subject to ever-increasing threats from climate change and other more direct anthropogenic disturbances [11,12].

Background mortality agents can trigger complex responses in corals that may affect colony physiological condition, alter demographic performance, especially growth [13–15] and reproduction [15,16,17] and they can therefore have significant consequences on the ability of colonies to withstand and survive periodic acute disturbances and environmental changes [18]. Intraspecific competition, for example, can substantially reduce fitness and growth rates of colonies engaged in competitive interactions [14]. Tanner 1997 documented a reduction in growth rates from 120 to 35% in *Acropora hyacinthus* when engaged in competitive interactions, and a decrease in growth from 45 to −16% in *Pocillopora damicornis*. Similarly, chronic predation can inflict a significant energetic cost to prey corals and may accelerate rates of coral decline following a disturbance [19]. Coral grazing fishes are a potentially important source of background coral mortality [19], even when they do not leave any visible signs of damage on coral colonies [20]. Rates of tissue removal from individual coral colonies can be considerable (16.75±0.30 bites per 20 min, [19]) and this chronic removal of live tissue can have potentially important consequences for colony fitness. Similarly, sedimentation can affect coral physiological condition by exerting significant energetic costs due to the removal of particles from colonies and limit energy availability due to reduced light and photosynthetic activity [15,21]. *Siderastrea siderea* reduced linear extension rates from 3.5 mm to 3 mm three years following an oil spill, which caused increased sedimentation levels [21].

The physiological condition of a colony is largely determined by the energy available and by the partitioning of energy reserves among maintenance, growth, and reproduction [22]. Energy within a colony is a limited resource and it is distributed among costly life history processes. If a coral invests heavily in repairing tissues damaged by chronic predation or sedimentation, or is investing heavily in interspecific competition, then this will reduce resources available for growth and reproduction. Evidences of energy trade-offs have been widely documented in corals, with injury often causing a decline in growth [23,24] or fecundity [25]. Moreover, diversion of essential energy reserves may undermine the capacity of corals to withstand periodic acute disturbances, such as anomalous temperatures that cause widespread bleaching [22]. When injured, corals often divert energy towards regeneration of lost tissue, and species with high regenerative capacity (such as *Acropora* spp) being able to fully heal the injury in less than 80 days [23]. However, environmental stresses, large lesions and competition may impair regeneration and hence compromise survival [23,26]. The bare skeleton resulting from tissue loss can be colonized by algae, pathogens or bioeroders, which may undermine the integrity of the colony [27,28]. These organisms may later compete with the coral for food and space, or cause structural damage to the coral skeleton [27,28].

The capacity of corals to withstand ongoing disturbances is strongly size-dependent, with small colonies being more vulnerable to whole-colony mortality than larger ones [6]. Corals as modular organisms are made up of repeated units (polyps), each of which can function and survive as physiologically independent entities. However, partial mortality and the consequent decline in the total number of polyps that make up a colony can greatly reduce individual fitness and resilience [6,17,29]. A reduction in size results in fewer polyps available to support colony vital processes and will generally reduce survivorship [6,30], growth [23,24], reproduction and regeneration [15]. Large colonies have greater regenerative abilities [6,8], growth [31], are more fecund [17] and have lower rates of total mortality compared to smaller colonies [6,17]. Likelihood of survival in larger colonies is greater than smaller ones because there is a higher probability that part of the colony may remain unaffected [32]. Particularly, following a disturbance, big colonies can make a disproportionate contribution to population as they produce more eggs per unit area [17].

Intra-specific variation of corals in responses to stresses is largely due to genotypic and phenotypic variation among both corals and their zooxanthellae [33–35], however the disturbance history and current physiological condition of individual colonies may also play a critical role. The exhaustion of energy available to maintain vital processes represents a physiologically critical threshold for survival [36]. During a bleaching event for instance, a key determinant for survival and recovery of a coral is its amount of lipid reserves [22], as they can. When bleaching occurs the energy acquisition by the zooxanthellae stops, hence the coral must use its energy reserves accumulated in the form of lipids in order to survive [38–41]. So colonies in good physiological conditions, with a great magnitude of lipid reserves, are more likely to survive and recover from a bleaching event, than colonies with lower level of lipid reserves [22,42]. Also colonies which survived a previous disturbance and are potentially in good physiological condition, can substantially contribute to community recover through their growth and through their reproductive output [17,43,44].

The purpose of this study is to quantify intra-specific variation in physiological condition (specifically, total lipid content and zooxanthellae density) through time in adult colonies exposed to several biological and environmental factors. Variation in colony condition among individuals may account for differences in susceptibility to disturbances. Many studies have documented significant variation in the capacity of corals to withstand and recover from major disturbances [4,8,45,46], but the underlying basis of this variation is still poorly understood. Most of these studies have focused on among-species variability for stress resistance. Hoegh-Guldberg [47] suggested that in the aftermath of climate change some coral species are more likely to adapt and survive better than others. But still little is known on intraspecific variability to environmental changes.

Methods

Ethics Statement

The activities for this study were conducted under permission from the Great Barrier.

Reef Marine Park Authority (Permit Number G12/35017.1). Visual censuses of fishes and benthic communities were conducted during this study; one coral branch per colony was collected in May and one in October.

Chronic Disturbances

This study was conducted at Lizard Island (14°40′S, 145°27′E) in the northern Great Barrier Reef, Australia. 24 colonies, ranging in size from 9 cm up to 35 cm diameter, of *Pocillopora damicornis* and *Acropora spathulata* were individually tagged and sampled in May and October 2012 to test for intraspecific differences in physiological condition. At the same time, detailed observations were undertaken to quantify intra-specific differences in background disturbance regimes (NB. There were no major bleaching events or other acute disturbances during the conduct of this study). Colonies at the same depth were selected from the reef crest in two different sites, one sheltered and one in the windward side of the island. For each coral colony we measured the distance from the reef crest (presumed to reflect colony physical position in respect of local hydrodynamic regime), proportional tissue loss attributable to coral competition and/or coral disease, and also rates of predation by corallivorous fishes. Variation in the level of predation among individual coral colonies was documented using GoPro cameras, deployed to record the total number of bites taken by all corallivorous fishes within replicate one-hour periods. The fish species and size were also recorded. Partial mortality was measured by quantifying the exact proportion of dead versus living tissue within the overall physical extent of each coral colony, using the software Image J. Growth rates were also calculated comparing colony surface area from pictures in May and in October for each individual colony.

Colony Physiological Condition

Colony condition was assessed based on total lipid content and zooxanthellae density. The size of lipid reserves is a good measure of colony condition because it represents an alternative source of fixed carbon, which can be allocated to vital processes such as growth or reproduction. Lipid reserves can also allow the host to meet its daily metabolic energy needs in absence of endosymbionts, such as during a bleaching event [42]. Similarly, the symbiotic relationship between the coral colonies and the symbionts makes zooxanthellae density a good proxy of coral condition [48]. Zooxanthellae density has been shown to decrease in response to chronic stresses such as exposure to both low and high temperature [49], sedimentation [50], disease [51], and water quality [52,53], and has been widely measured to assess coral condition in response to stimulants, as well as natural variation in environmental factors [52,53,54,55]. To measure both total lipid content and zooxanthellae density, one branch was collected from each of the tagged colony in May and October. To minimize within-branch variability in lipids, only central inner branches were collected [56].

Branches were fixed in 10% formalin seawater and decalcified in 5% Formic acid for 1 day followed by 10% formic acid for 5 days and then stored in 70% ethanol. To extract total lipids, coral branches were dried in the oven at 55°C for 24 h, weighed and placed in a solution of chloroform: methanol (2:1, v:v) to dissolve the lipids [57]. The tissues were redried at 55°C overnight and reweighed. The difference in weight was due to lipids loss, with total lipid content then expressed as percentage of dry weight. Total lipid content was analysed instead of lipid classes because of the total lipids, triacylglycerol and wax esters are the main storage lipids in corals, and can account for 40–73% of total lipids [58–60].

Zooxanthellae density (per unit surface area (cells/cm^2)) was quantified for each coral based on samples (5 mm×5 mm) from the collected branch (4 replicates per branch). Each sample was homogenized and the ground solution was examined on a glass slide under a microscope and counts were normalized to coral surface area, following McCowan et al. [61].

Data were deposited on Figshare and are available at http://dx.doi.org/10.6084/m9.figshare.928440.

Data Analyses

To test whether there were significant differences in partial mortality, in total lipid content, in zooxanthellae density, in competition and in the number of fish bites, between May and October, a series of paired t-tests were carried out for each variable. Proportional mortality of individual coral colonies was Arcsin transformed prior to analyses. A One-Way ANOVA was carried out to further investigate whether colonies exposed to predation had lower lipid content than colonies that did not receive any bite. To test whether physiological condition of coral colonies relates to biological and physical disturbance regimes, we used a stepwise Multiple Regression model, testing the extent to which i) partial mortality, 2) mean number of fish bites, 3) extent of coral competition, 4) colony size, 5) distance from crest, and 6) Site, explained intraspecific variation in either total lipid content or zooxanthelae density for each coral species. Separate analyses were carried out for total lipid content and zooxanthellae density. Bivariate correlations were also used to test for any relationship between zooxanthellae density and total lipid content in each coral species.

Results

Chronic Disturbances

Competitive interactions and partial mortality were constant between May and October in both coral species (Fig. 1). Only the number of fish bites differed significantly with time, being 23 times higher in October than in May for *P. damicornis* (paired t-test, $p < 0.05$). Some colonies received few bites in May (from 0 to 4 bites per hour) while they were exposed to high predation pressure in October (163 and 392 bites per hour). In *A. spathulata*, overall predation pressure was two times higher in October, but given marked intra-specific variation this was not statistically significant (Fig. 1). Bite rate varied among colonies in *P. damicornis*, ranging from 0 to >100 bites per hour among colonies. In both coral species, the colonies that received most bites in May were not the same ones that received most bites in October, while some colonies did not receive any bite in either May or October.

In *P. damicornis* the majority of the colonies were smaller than 1000 cm^2, with colony surface area ranging from 161 cm^2 to 679 cm^2, while in *A. spathulata* colony surface area ranged from 160 cm^2 up to 1.830 cm^2. Colony growth (expressed as changes in colony surface area) from May to October in *A. spathulata* was 118.3 cm^2, while *P. damicornis* showed a negative growth rate (-10.3 cm^2) due to partial mortality.

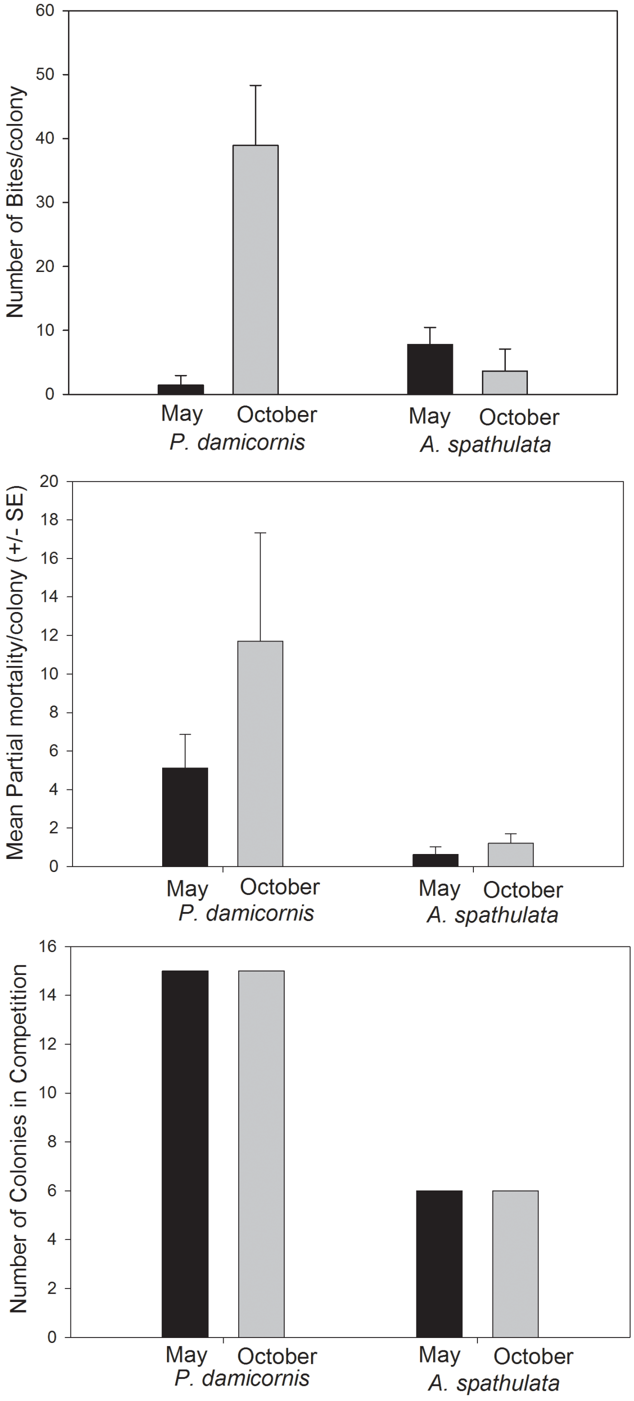

Figure 1. Chronic disturbance regimes in May and October in the two reef-building corals *P. damicornis* and *A. spathulata*. A) Predation – mean no. of bites taken per colony in replicate three-minute observations, where Go Pro cameras were used to record the total number of bites taken by all corallivorous fishes (mostly, butterflyfishes), B) Partial mortality –proportional of dead versus living tissue within the overall physical extent of each coral colony, C) – number of colonies engaged in competitive interactions.
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Intraspecific Variation in Colony Condition

All the sampled corals survived the entire study period. Colony condition was found to vary between May and October in both coral species (Fig. 2). Specifically, a significant decline in total lipid content was observed in October compared to May (Table 1, 2; Fig. 2). In *A. spathulata* energy reserves in October were almost half compared to May (declined from 13.7 (±7.5) % to 7.8 (±1.8) %), while in *P. damicornis* the decline was two-fold during the same time (Fig. 2). Zooxanthellae density on the other hand, remained constant and did not change significantly between sampling periods in either coral species (Fig. 2). For *P. damicornis*, intraspecific variation in total lipid content was strongly correlated with zooxanthellae density ($r = 99$, $df = 5{,}42$, $p < 0.001$), but no such relationship was found for *A. spathulata*.

P damicornis showed a high variation within colonies in partial mortality (between 0 and 20%), number of fish bites (between 0 and 392 bites per hour) and total lipid content (between 1.5 and 80% dw). By comparison, intraspecific variation in partial mortality and disturbance rates for *A. spathulata* were much smaller (Fig. 1).

In *P damicornis*, partial mortality, number of fish bites, competition, distance from crest and size were poor predictors of both lipid content (Multiple Regression total lipid content $r^2 = 11$, $df = 5{,}42$, $p = 0.27$; Table 1); and zooxanthellae density ($r^2 = 25$, $df = 5, 42$, $p = 0.3$; Table 1): the regressions explained only a very small proportion of the total variation (<12%). Conversely in *A. spathulata*, partial mortality and distance from crest were found to have a significant effect on both total lipid content and zooxanthellae density (Multiple Regression total lipid content *A. spathulata* $r^2 = 14$, $df = 5{,}42$, $p = 0.2$; zooxanthellae density $r^2 = 26$, $df = 5{,}42$, $p = 0.02$; Table 2). In particular, total lipid content increased with distance from crest, while zooxanthellae density declined with increasing partial mortality and distance from crest (Table 2).

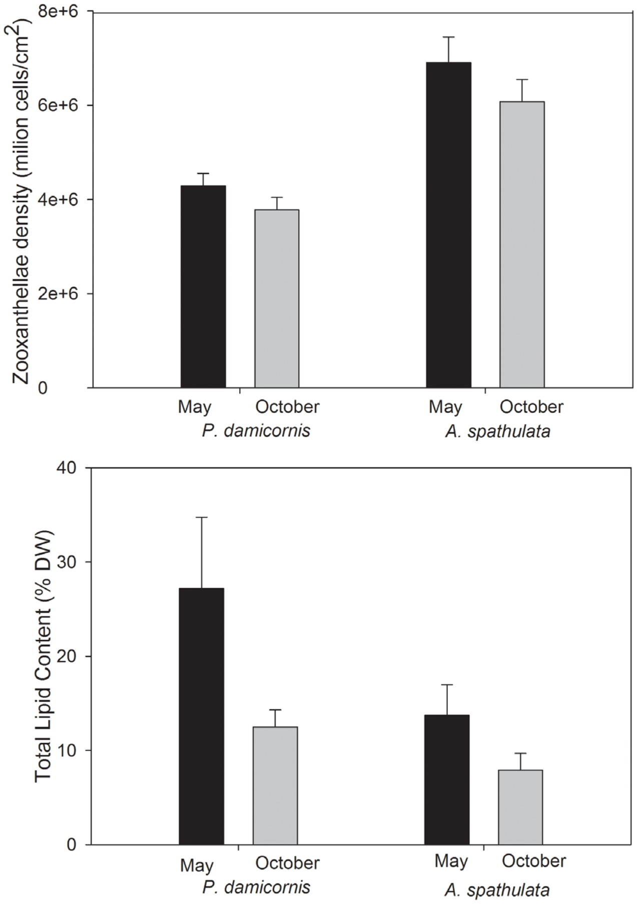

Figure 2. Physiological condition, specifically A) total lipid content and B) zooxanthellae density, in May and October in the two reef-building corals *P. damicornis* and *A. spathulata*.
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Discussion

This is the first study that attempts to relate intraspecific variation in physiological condition of scleractinian corals to small-scale differences in chronic disturbances, such as fish predation. It is well known that coral colonies living in close proximity may exhibit vastly different demographic rates [6,8,45,62], possibly reflective of differences in their disturbance history and subsequent energy allocation [27,63]. The difficulty in making this link is that very subtle differences in disturbance regimes, operating at any time in the lifetime of each coral, may lead to marked differences in contemporary condition and fitness of individual coral colonies. We acknowledge that the current study provides very limited insights on lifetime differences among closely positioned colonies, mainly due to the limited observational periods, and the range of factors that may be impacting on individual coral colonies. However, it is interesting that we saw no significant temporal shifts in rates of partial mortality, competition and predation between the two observational periods. The high degree of constancy in background mortality may be evidence that there is a high stability in terms of routine mortality.

Under low levels of background mortality, demographic models of scleractinian corals predict constant growth and fecundity of individual colonies, enabling rapid recovery following major acute disturbance [4,36,64]. However, in the present study, even within relatively constant rates of biological and physical disturbances, the incidence of injuries still varied among colonies. For instance, some coral colonies did not receive any fish bites in either May or October. Similarly, some colonies of *P. damicornis* that were not injured in May showed partial mortality in October, while some colonies never showed partial mortality. In the long term, these differences among colonies may likely be responsible for important inter-colony differences in condition and fitness. Importantly, variation in the disturbance history of individual colonies may have important ramifications for their long-term fate, especially during major disturbances (e.g., climate-induced coral bleaching).

Not unexpectedly, this study revealed marked intraspecific variation in the physiological condition of both *A. spathulata* and *P. damicornis*. However, these differences were only partially explained by inter-colony differences in rates of partial mortality, competition, predation, colony size or the position of the colony relative to the reef crest. Comparing to other studies, which documented a lipid level of 35% in tissue of *P. damicornis* [56,65], this study found a lower lipid content (27% dw). Conversely, zooxanthellae density was found to be higher (3.0 cells/cm^2 in May) than what reported in the literature (3.0 cells/cm^2, [66]). Also differences in colony condition, specifically in total lipid content, were greater among adjacent colonies of *P. damicornis* than when compared to colonies of *A. spathulata*, revealing intraspecific differences in physiological condition and in susceptibility to chronic disturbances. These differences suggest that coral physiological condition can be more variable than predicted with the outcome depending, in part, on flow, partial mortality, and position of the colony.

Predation rates on coral colonies were higher in October than in May in both coral species, especially in *P. damicornis*. Similarly,

Table 1. Multiple Regression for zooxanthellae density and total lipid content in *P. damicornis*.

Zooxanthellae	**B**	**StdErr of B**	**t(42)**	**p**
Intercept				
Partial Mortality	−14	834221	−1.7	0.08
Competition	−44	312617	−1.4	0.1
Number of bites	1632	2745	0.5	0.5
Size	174	1044	0.16	0.8
Site	2338	374570	0.06	0.9
Distance from crest	68	61603	1.1	0.2
Lipid content	**B**	**StdErr of B**	**t(42)**	**p**
Intercept				
Partial Mortality	−23	13.7	−1.7	0.09
Competition	−3.6	5.1	−0.7	0.4
Number of bites	0.008	0.04	0.1	0.8
Size	0.003	0.01	−1.7	0.8
Site	3.96	6.14	0.64	0.5
Distance from crest	−1.6	1.01	−1.5	0.1

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coral grazing parrotfishes have been shown to exhibit higher feeding rates in October compared to April on the GBR [67]. For parrotfishes, temporal differences in feeding rates have been previously attributed to differences the nutritional quality of colonies associated with gametogenesis [68]. For butterflyfishes, which tend to take very shallow bites [69], it is unlikely that gametogenesis of the corals would influence feeding behavior, but changes in the nutritional content may still occur within and among coral colonies. For instance mucus production can drive feeding preferences in butterflyfishes [70,71]. In October, colonies may have released more mucous as a stress response to environmental changes [72] and this discharge may have increased their desirability as food source. The observed differences in bite rates could also be due to seasonal differences in the metabolic rate of food demands of the fishes themselves.

Chronic disturbances were found to affect physiological condition only in. *A. spathulata*, which exhibited strong intraspecific variation that was explained to a large extent by inter-colony differences in biological disturbances and physical position, however these differences were not observed in *P. damicornis*. Even though both study species (*A. spathulata* and *P. damicornis*) are shallow, fast-growing, branching corals, they have slightly different

Table 2. Multiple Regression for zooxanthellae density and total lipid content in *A. spathulata*.

Zooxanthellae	**B**	**StdErr of B**	**t(18)**	**p**
Intercept				
Partial Mortality	−7386077	2909017	−2.5	0.01
Competition	−543263	551519	−0.98	0.3
Number of bites	22837	19454	1.17	0.24
Size	−487	643	−0.75628	0.4
Site	−510264	500279	−1.019	0.3
Distance from crest	−121255	55915	−2.16854	0.03
Lipid content	**B**	**StdErr of B**	**t(42)**	**p**
Intercept				
Partial Mortality	−2.1	18.5127	−0.11	0.9
Competition	0.7522	3.5098	0.21	0.8
Number of bites	−0.04	0.1238	0.33	0.7
Size	0	0.004	−0.05	0.9
Site	−1.87	3.2105	−0.58	0.5
Distance from crest	0.9	0.3558	2.57	0.01

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life-histories strategies, which can explain observed differences. *P. damicornis* is a brooding, opportunistic coral which colonizes very disturbed habitats and it is one of the most resilient corals [46]. These characters may explain why *P. damicornis* was more resilient to chronic background disturbances than *A. spathulata*, which instead seems to dominate communities in relatively stable environments [46]. *A. spathulata* showed higher lipid reserves with increasing distance from the crest and lower symbiont density with increasing partial mortality and distance from crest. The observed increase in total lipid content with distance from crest may be due to the higher energetic cost of this reef habitat.

The reef crest is a shallow wave-exposed habitat, where water flow strongly influences organisms mechanically and physiologically with important consequences on community structure [73]. To avoid hydrodynamic dislodgment, colonies on the crest may need to invest more resources in growth to reach the dislodgment threshold [73], but since energy is limited within a colony, if more resources are allocated to increase colony size, less energy will be available to store. The findings from this study suggest that colonies in intermediate position between reef crest and reef flat have a better performance than conspecific on the crest. However, even though the reef crest is an energetic costly habitat, the high flow can positively affect colonies as they can benefit from it for feeding and escretion [74]. Together with light, flow is a critical abiotic factor affecting colony condition [74]. Colonies exposed to high flow generally have higher skeletal density, higher protein concentration, zooxanthellae density, chlorophyll content, and higher number and size of oocytes compared to colonies exposed to lower flow conditions [74]. Flow enhances zooxanthellae density and photosynthesis due to the enhanced nutrient supply [75], and can explain the decreasing zooxanthellae density with distance from crest found in this study.

The symbiotic relationship between the zooxanthellae and the host may be affected by a variety of internal and external factors and processes, the composition of which still has not been fully investigated [54,76]. Findings from this study suggest that increasing partial mortality and distance from crest may lead to a decline in density of *Symbiodinium*. Not many studies have shown differences in zooxanthellae density among reef habitats regardless of depth. For instance Strickland [76] did not find any difference in zooxanthellae density with increasing distance from the reef crest or location along the reef. Conversely, zooxanthellae within the same reef habitat have been shown to vary with environmental fluctuations and season cycles [54,77,78].

Despite consistency in levels of routine or background mortality, the lipid content within coral tissues consistently declined across all coral colonies between May and October in both *P. damicornis* and *A. spathulata*. The decline in total lipid content observed in October in both coral species may partly be explained by sustained and ongoing rates of background mortality, though the declines in may also reflect limited productivity during winter months, due to both reduced temperature and reduced day length [79]. Zooxanthellae supply corals with an excess of lipids and a limitation in their activity can results in a decline in lipid reserves [56,80]. Stimson [56] documented a decrease in total lipid content following about one month in *P. damicornis* due to light limitation. Corals tend to consume their lipid reserves when maintenance costs of a colony exceed carbon acquisition [22], during environmental unfavourable conditions such as limited light [6,58,81], during reproductive events [82–84] or whenever an increase in energy demand occurs such as the development of a tumor in coral tissue [85].

Large colonies generally have greater regenerative abilities [6,8], greater growth [31], are more fecund [17] and have lower rates of total mortality compared to smaller colonies [6,15]. Consequently we were expecting larger colonies to be more resilient to chronic background disturbances than smaller ones. Conversely, in the present study chronic disturbances had a similar effect on physiological condition of colonies regardless of the size, suggesting that larger colonies are not necessary more resilient than smaller colonies. Similar incidence of chronic disturbances on coral colonies regardless of the size also suggests a lack of size-specific susceptibility to agents of coral mortality [86]. Other studies documented a lack of differences in resilience between small and large colonies [87,88]. For instance *S. siderea* exposed to partial mortality continued to dedicate resources to reproduction even after the colony had shrunk below their size of maturation while larger colonies reduced their fecundity [88]. Often recent injuries play a bigger role than size in predicting colony fate [89]. Large colonies with higher partial mortality may die before small colonies with no injuries [89].

Extensive research effort has focused on understanding the ability of reef corals to withstand and absorb disturbances, thereby contributing to the persistence and resilience of coral colonies, populations and species [1,3,12,42,49,90,91]. Quantifying the effects of essentially routine and ongoing disturbances on colony condition and assess intraspecific differences in colony condition added to this understanding and it is critical because background mortality influences recovery capacity, time and vulnerability to future disturbances.

This study documented significant effects of partial mortality and distance from crest on zooxanthellae density in *A. spathulata* with important ecological consequences for recovery capacity in the aftermath of climate change. A reduction in performances arising from these sub-lethal stressors, is likely to reduce colony resilience and hence increase chances of whole-colony mortality so that colonies suffering from partial mortality may not survive a subsequent acute disturbance. The approach used here, investigating drivers of colony-condition and their energetic consequences for colony resilience, provides a strong framework for predicting resistance, recovery capacity and resilience of reef-building corals. If colonies in poor physiological conditions (e.g. less resilient) are more susceptible to bleaching, disease and other stressors, colonies capable of maintaining a higher physiological condition may have a distinct ecological advantage [22,92]. Consequently, colonies of *A. spathulata*, with high partial mortality rates and located on the reef crest, may have a lower potential to withstand and recover from environmental changes compared to conspecific with lower rates of partial mortality and located in intermediate habitats. The observed differences in physiological conditions could have a strong bearing on the selectivity of major disturbances and the capacity of corals to withstand major disturbances, and thereby adapt to changing conditions.

This study is the first to document significant intra-specific variation in background mortality and colony condition, the next step is to investigate whether this variation impacts individual vulnerability of corals. If so, this will provide strong incentive to reduce background levels of stresses (e.g. control all the factors that routinely injure colonies such as predation or anchoring) as a sure way to increase resilience of corals subject to inevitable increases in acute disturbances in association with global climate change.

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Author Contributions

Conceived and designed the experiments: CP KA MSP. Performed the experiments: CP KA MSP. Analyzed the data: CP KA MSP. Contributed reagents/materials/analysis tools: CP KA MSP. Wrote the paper: CP KA MSP.

References

1. Karlson RH, Hurd LE (1993) Disturbance, coral reef communities, and changing ecological paradigms. Coral Reefs 12: 117–125.
2. Stimson J (1985) The effect of shading by the table coral *Acropora hyacinthus* on understory corals. Ecology 66: 40–53.
3. Connell JH (1997) Disturbance and recovery of coral assemblages. Coral Reefs 16 Suppl: S101– S113.
4. Wakeford M, Done TJ, Johnson CR (2008) Decadal trends in a coral community and evidence of changed disturbance regime. Coral Reefs 27: 1−13.
5. Pratchett MS, Pisapia C, Sheppard C (2013) Background mortality rates for recovering populations of *Acropora cytherea* in the Chagos Archipelago, central Indian Ocean. Mar Environ Res 86: 29–34.
6. Hughes TP, Jackson JBC (1985) Population dynamics and life histories of foliaceous corals. Ecol Monogr 55: 141–166.
7. Knowlton N, Lang JC, Keller BD (1990) Case study of natural population collapse: post-hurricane predation on Jamaican staghorn corals. Washington: Smithsonian Institution Press.
8. Bythell JC, Gladfelter EH, Bythell M (1993) Chronic and catastrophic natural mortality of three common Caribbean reef corals. Coral Reefs 12: 143–152.
9. Bak RPM, Luckhurst BE (1980) Constancy and change in coral reef habitats along depth gradients at Curaçao. Oecologia 47: 145–155.
10. Harriot VJ (1985) Mortality rates of scleractinian corals before and during a mass bleaching event. Mar Ecol Prog Ser 21: 81–88.
11. Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, et al. (2003) Climate change, human impacts, and the resilience of coral reefs. Science 301: 929−93.
12. Déath G, Fabricius KE, Sweatman H, Puotinen M (2012) The 27-year decline of coral cover on the Great Barrier Reef and its causes. Proc Natl Acad Sci 109: 17995–17999.
13. Cox EF (1986) The effects of a selective corallivore on growth rates and competition for space between two species of Hawaiian corals. J Exp Mar Biol Ecol 101: 161–174.
14. Tanner JE (1997) Interspecific competition reduces fitness in scleractinian corals. J Exp Mar Biol Ecol 214: 19–34.
15. Henry LA, Hart M (2005) Regeneration from injury and resource allocation in sponges and corals– a review. Int Rev Hydrobiol 90: 125–158.
16. Strauss SY, Agrawal AA (1999) The ecology and evolution of plant tolerance to herbivory. Trends Ecol Evol 14: 179–185.
17. Hall VR, Hughes TP (1996) Reproductive strategies of modular organisms: comparative studies of reef-building corals. Ecology 77: 950–963.
18. Rotjan RD, Dimond JL, Thornhill DJ, Leichter JJ, Helmuth B, et al. (2006) Chronic parrotfish grazing impedes coral recovery after bleaching. Coral Reefs 25: 361–368.
19. Cole AJ, Lawton RJ, Pratchett MS, Wilson SK (2011) Chronic coral consumption by butterflyfishes. Coral Reefs 30: 85–93.
20. Hourigan TF, Tricas TC, Reese ES (1988) Coral reef fishes as indicators of environmental stress in coral reefs. In: Soule DF, Kleppel GS, editors. Marine Organisms as Indicators. New York: Springer Verlag. 107–135.
21. Guzman HM, Burns KA, Jackson JBC (1994) Injury, regeneration and growth of Caribbean reef corals after a major oil spill in Panama. Mar Ecol Prog Ser 105: 231–241.
22. 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. Funct Ecol 23: 539–550.
23. Bak RPM (1983) Neoplasia, regeneration and growth in the reef-building coral *Acropora Palmata*. Mar Biol 77: 221–227.
24. Meesters EH, Noordeloos M, Bak RPM (1994) Damage and regeneration: links to growth in the reef-building coral *Montastrea annularis*. Mar Ecol Prog Ser 112: 119–128.
25. Kojis BL, Quinn NJ (1985) Puberty in *Goniastrea favulus* age or size limited? Proc 5th Int Coral Reef Congr 4: 289–293.
26. Meesters EH, Bos A, Gast GJ (1992) Effects of sedimentation and lesion position on coral tissue regeneration. Proc 7th Int Coral Reef Symp 2: 681–688.
27. Bak RPM, Brouns JJWM, Heys FML (1977) Regeneration and aspects of spatial competition in the scleractinian corals *Agaricia agaricites* and *Montastrea annularis*. Proc 3rd Int Coral Reef Symp 143–148.
28. Titlyanov EA, Titlyanova TV, Yakovleva IM, Nakano Y, Bhagooli R (2005) Regeneration of artificial injuries on scleractinian corals and coral/algal competition for newly formed substrate. J Exp Mar Biol Ecol 323: 27–42.
29. Bruckner AW, Hill RL (2009) Ten years of change to coral communities off Mona and Desecheo Islands, Puerto Rico, from disease and bleaching. Dis Aquat Organ 87: 19–31.
30. Babcock RC (1991) Comparative demography of three species of scleractinian corals using age and size-dependent classifications. Ecol Monogr 61: 225–244.
31. Hughes TP, Jackson JBC (1980) Do corals lie about their age? Some demographic consequences of partial mortality, fission, and fusion. Science 209: 713−715.
32. Jackson JBC (1979) Morphological strategies of sessile animals. In: Larwood G, Roser BR, editors. Biology and systematics of colonial organisms. London: Academic Press. 499–555.
33. Black NA, Voellmy R, Szmant AM (1995) Heat shock protein induction in *Montastrea faveolata* and *Aiptasia pallida* exposed to elevated temperatures. Biol Bull 188: 234–240.
34. Baker AC, Rowan R (1997) Diversity of symbiotic dinoflagellates (zooxanthellae) in scleractinian corals of the Caribbean and eastern Pacific. Proc 8th Int Coral Reef Symp 2: 1301–1306.
35. D'Croz L, Maté JL (2004) Experimental responses to elevated water temperature in genotypes of the reef coral *Pocillopora damicornis* from upwelling and non-upwelling environments in Panama. Coral Reefs 23: 473–483.
36. Gurney WSC, Middleton DAJ, Nisbet RM, McCauley E, Murdoch WM, et al. (1996) Individual energetics and the equilibrium demography of structured populations. Theor Popul Biol 49: 344–368.
37. Spencer-Davies P (1991) Effect of daylight variations on the energy budgets of shallow-water corals. Mar Biol 108: 137–144.
38. Szmant AM, Gassman NJ (1990) The effects of prolonged "bleaching" on the tissue biomass and reproduction of the reef coral *Montastrea annularis*. Coral Reefs 8: 217–224.
39. 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. Limnol Oceanogr 45: 677–685.
40. 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. Mar Biol 145: 621–631.
41. Rodrigues LJ, Grottoli AG (2007) Energy reserves and metabolism as indicators of coral recovery from bleaching. Limnol Oceanogr 52: 1874–1882.
42. Grottoli AG, Rodrigues LJ, Palardy JE (2006) Heterotrophic plasticity and resilience in bleached corals. Nature 440: 1186–1189.
43. Halford A, Cheal AJ, Ryan D, Williams D (2004) Resilience to large-scale disturbance in coral and fish assemblages on the Great Barrier Reef. Ecology 85: 1892–1905.
44. Connell JH, Hughes TP, Wallace CC, Tanner JE, Harms KE, et al. (2004) A long-term study of competition and diversity of corals. Ecol Monogr 74: 179–210.
45. Baird AH, Marshall PA (2002) Mortality, growth and reproduction in scleractinian corals following bleaching on the Great Barrier Reef. Mar Ecol Prog Ser 237: 133–141.
46. Darling ES, Alvarez-Philip L, Oliver TA, McClanahan TR, Côté IM (2012) Evaluating life-history strategies of reef corals from species traits. Ecol Lett 15: 1378–1386.
47. Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. Mar Freshwater Res 50: 839–66.
48. Sheppard CRC, Davy SK, Pilling GM (2009) The biology of coral reefs. Oxford New York: Oxford University Press.
49. Baker AC, Glynn PW, Riegl B (2008) Climate change and coral reef bleaching: an ecological assessment of long-term impacts, recovery trends and future outlook. Estuar Coast Shelf S 80: 435–471.
50. Peters EC, Pilson MEQ (1985) A comparative study of the effects of sedimentation on symbiotic and asymbiotic colonies of the coral *Astrangia danae* Milne-Edwards and Haime 1849. J Exp Mar Biol Ecol 92: 215–230.
51. Cervino J, Goreau TJ, Nagelkerken I, Smith GW, Hayes R (2001) Yellow band and dark spot syndromes in Caribbean corals: distribution, rate of spread, cytology, and effects on abundance and division rate of zooxanthellae. Hydrobiologia 460: 53–63.
52. Cooper TF, Gilmour JP, Fabricius KE (2009) Bioindicators of changes in water quality on coral reefs: review and recommendations for monitoring programmes. Coral Reefs 28: 589–606.
53. Cooper TF, Ulstrup KE (2009) Mesoscale variation in the photophysiology of the reef building coral *Pocillopora damicornis* along an environmental gradient. Estuar Coast Shelf S 83: 186–196.
54. Fagoonee I, Wilson HB, Hassell MP, Turner JR (1999) The dynamics of zooxanthellae populations: a long-term study in the field. Science 283: 844–845.
55. Ferrier-Pagès C, Schoelzke V, Jaubert J, Muscatine L, Hoegh-Guldberg O (2001) Response of a scleractinian coral, *Stylophora pistillata,* to iron and nitrate enrichment. J Exp Mar Biol Ecol 259: 249–261.
56. Stimson JS (1987) Location, quantity and rate of change in quantity of lipids in tissue of Hawaiian hermatypic corals. Bull Mar Sc 41: 889–904.
57. Barnes DJ, Blackstock J (1973) Estimation of lipids in marine animals and tissues: detailed investigation of the sulphophospho- vanillin method for 'total' lipids. J Exp Mar Biol Ecol 112: 103–118.
58. Harland AD, Navarro JC, Spencer Davies P, Fixter LM (1993) Lipids of some Caribbean and Red Sea corals: total lipid, wax esters, triglycerides and fatty acids. Mar Biol 117: 113–117.

59. Patton JS, Abraham S, Benson AA (1977) Lipogenesis in the intact coral *Pocillopora capitata* and its isolated zooxanthellae: evidence for a light-driven carbon cycle between symbiont and host. Mar Biol 44: 235–247.
60. Oku H, Yamashiro H, Onaga K, Sakai K, Iwasaki H (2003) Seasonal changes in the content and composition of lipids in the coral *Goniastrea aspera*. Coral Reefs 22: 83–85.
61. McCowan DM, Pratchett MS, Paley AS, Seeley M, Baird AH (2011) A comparison of two methods of obtaining densities of zooxanthellae in *Acropora millepora*. Galaxea Journal of Coral Reef Studies 13: 29–34.
62. Hughes TP (1994) Catastrophes, phase-shifts, and large-scale degradation of a Caribbean coral reef. Science 265: 1547–1551.
63. Hall VR (1997) Interspecific differences in the regeneration of artificial injuries on scleractinian corals. J Exp Mar Biol Ecol 212: 9–23.
64. Done TJ (1988) Simulation of recovery of pre-disturbance size structure in populations of *Porites* spp. damaged by the crown of thorns starfish *Acanthaster planci*. Mar Biol 100: 51–61.
65. Ward S (1995) Two patterns of energy allocation for growth, reproduction and lipid storage in the scleractinian coral *Pocillopora damicornis*. Coral Reefs 14: 87–90.
66. Stimson JS (1997) The annual cycle of density of zooxanthellae in the tissues of field and laboratory-held *Pocillopora damicornis* (Linnaeus). J Exp Mar Biol Ecol 214: 35–48.
67. Bonaldo RM, Welsh JQ, Bellwood DR (2012) Spatial and temporal variation in coral predation by parrotfishes on the GBR: evidence from an inshore reef. Coral Reefs 31: 263–272.
68. Rotjan RD, Lewis SM (2009) Predators selectively graze reproductive structures in a clonal marine organism. Mar Biol 156: 569–577.
69. Motta PJ (1988) Functional morphology of the feeding apparatus of ten species of Pacific butterflyfishes (Perciformes, Chaetodontidae): An ecomorphological approach. Environ Biol Fish 22: 39–67.
70. Cole A, Pratchett MS, Jones GP (2009) Effects of coral bleaching on the feeding response of two species of coral-feeding fish. J Exp Mar Biol Ecol 373: 11–15.
71. Pisapia C, Cole AJ, Pratchett MS (2012) Changing feeding preferences of butterflyfishes following coral bleaching. Proc 12th Int Coral Reef Sym 13: 1–5.
72. Reigl B, Branch GM (1995) Effects of sediment on the energy budgets of four scleractinian (Bourne 1900) and five alcyonacean (Lamouroux 1816) corals. J Exp Mar Biol Ecol 186: 259–275.
73. Madin JS, Dell AI, Madin EMP, Nash MC (2013) Spatial variation in mechanical properties of coral reef substrate and implications for coral colony integrity. Coral Reefs 32: 173–179.
74. Mass T, Brickner I, Hendy E, Genin A (2011) Enduring physiological and reproductive benefits of enhanced flow for a stony coral. Limnol Oceanogr 56: 2176–2188.
75. Muscatine L, Falkowski PG, Dubinsky Z, Cook PA, McCloskey LR (1989) The effect of external nutrient resources on the population dynamics of zooxanthellae in a reef coral. Proc R Soc Lond B 236: 311–324.
76. Strickland D (2010) Variations in coral condition within the hydrodynamic regime at Sandy Bay, Ningaloo Reef, Western Australia. Thesis University Western Australia.
77. Rowan R, Knowlton N, Baker AC, Jara J (1997) Landscape ecology of algal symbionts creates variation in episodes of coral bleaching. Nature 388: 265–269.
78. Jones RJ (1997) Zooxanthellae loss as a bioassay for assessing stress in corals. Mar Ecol Prog Ser 149: 163–171.
79. Cooper T, Lai M, Ulstrup KE, Saunders SM, Flematti GR, et al. (2011) Symbiodinium genotypic and environmental controls on lipids in reef building corals. PLOSONE 6(5): e20434.
80. Crossland CJ, Barnes DJ, Borowitzka MA (1980) Diurnal lipid and mucus production in the staghorn coral *Acropora acuminata*. Mar Biol 60: 81–90.
81. Hoogenboom M, Rodolfo-Metalpa R, Ferrier-Pagès C (2010) Co-variation between autotrophy and heterotrophy in the Mediterranean coral *Cladocora caespitosa*. J Exper Biol 213: 2399–2409.
82. Richmond RH (1987) Energetics, competency, and long-distance dispersal of planula larvae of the coral *Pocillopora damicornis*. Mar Biol 93: 527–533.
83. Pernet V, Gavino V, Gavino G, Anctil M (2002) Variations of lipid and fatty acid contents during the reproductive cycle of the anthozoan *Renilla koellikeri*. J Comp Physiol B 172: 455–465.
84. Leuzinger S, Anthony K, Willis B (2003) Reproductive energy investment in corals: scaling with module size. Oecologia 136: 524–531.
85. Yamashiro H, Oku H, Onaga K, Iwasaki H, Takara K (2001) Coral tumors store reduced level of lipids. J Exp Mar Biol Ecol 265: 171–179.
86. Bak RPM, Meesters EH (1998) Coral population structure: the hidden information of colony-size frequency distribution. Mar Ecol Prog Ser 162: 301–306.
87. Nugues MM, Roberts CM (2003) Partial mortality in massive reef corals as an indicator of sediment stress on coral reefs. Mar Pollut Bull 46: 314–323.
88. Graham JE, van Woesik R (2013) The effects of partial mortality on the fecundity of three common Caribbean corals. Mar Biol 160: 2561–2565.
89. Cumming (2002) Tissue injury predicts colony decline in reef-building corals. Mar Ecol Prog Ser 242: 131–141.
90. Marshall PA, Baird AH (2000) Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. Coral Reefs 19: 155–163.
91. Linares C, Pratchett MS, Coker DJ (2011) Recolonisation of *Acropora hyacinthus* following climate-induced coral bleaching on the Great Barrier Reef. Mar Ecol Prog Ser 438: 97–104.
92. Bachok Z, Mfilinge P, Tsuchiya M (2006) Characterization of fatty acid composition in healthy and bleached corals from Okinawa, Japan. Coral Reefs 25: 545–554.