

Reviewer comment #1:

(Page 3, line 12) please replace “coral communities exposed” with “exposure of coral communities”.

Author response #1:

Agree – changed in revised manuscript

Reviewer comment #2:

(Page 3, line 20) Buxton’s paper is from 2012.

Author response #2: Agree – changed in revised manuscript

Reviewer comment #3:

(Page 3, lines 17-30) The listed studies and respective findings poorly represent available knowledge on this topic. The author should present an unbiased selection of relevant papers and especially avoid basing his literature review only on his own studies.

Author response #3:

I have modified the revised manuscript to include a brief description of the proposed ‘CO₂-limitation model’ of coral bleaching (sensu Fig. 1, adapted from [Wooldridge 2009](#)). The description explains how the model-predicted physiological impact(s) on host-symbiont relations is consistent (identical) with the downstream consequences of the ‘photoinhibition model’ of coral bleaching.

New text reads:

A cellular model for this warm-water breakdown of the coral–algae endosymbiosis has been developed in recent years and includes algal photoinhibition, oxidative damage and host-cell disruption as underlying processes ([Gates et al. 1992](#); [Lesser 1996](#); [Jones et al. 1998](#); [Warner et al. 1999](#)). Recently, [Wooldridge \(2009\)](#) outlined how this cellular model could be extended

to include the possibility that the bleaching response is initially triggered by a failure of the coral host to maintain a sufficient supply of CO₂ for its endosymbiont partner, particularly during periods of excess solar radiation when the photosynthetic demand for CO₂ is maximal. Theoretical considerations do permit CO₂ (sink) limitation within the 'dark reactions' of photosynthesis to be proposed as a potential trigger for the classic bleaching sequence of photoinhibition, oxidative damage and zooxanthellae expulsion (Fig. 1; [Wooldridge, 2009](#)). In this case: (i) lack of CO₂ substrate required for the 'dark reactions' can reduce the rate of consumption of the products of photosynthetic electron transport (ATP and NADPH), subsequently causing the photosynthetic electron transport components of the 'light reactions' to become blocked ([Takahashi and Murata 2006](#)); (ii) continued funnelling of excitation energy into the over-reduced electron transport chain can then trigger the onset of photoinhibition ([Jones and Hoegh- Guldberg 2001](#)), damage essential photosynthetic components, (principally photosystem II, PSII), and generate damaging reactive oxygen species (ROS) ([Lesser 1996](#); [Warner et al. 1999](#)); and (iii) the excess production of ROS beyond the antioxidant defence strategies of the coral host (and zooxanthellae) has been linked to the host-cell necrosis and detachment that underpins zooxanthellae expulsion ([Gates et al. 1992](#); [Dunn et al. 2002](#)). Importantly, this sequence of events is consistent with a growing body of evidence which indicates that that the 'dark reactions' of photosynthesis may be a primary site of thermal damage ([Jones et al., 1998](#); [Buxton et al., 2012](#)).

The potential for CO₂-limiting conditions to develop around the Rubisco enzyme of the zooxanthellae is given credibility by numerous findings which highlight that both photosynthesis and calcification in symbiotic reef corals is often carbon limited ([Herfort et al. 2008](#); [Marubini et al. 2008 + others](#)).....

Reviewer comment #4:

(Page 3, lines 28-30) I think the author needs to put in perspective the role of coral heterotrophy in bleaching susceptibility

Author response #4:

I have included an additional paragraph to the manuscript to explain how coral heterotrophy could be envisaged help to maintain the CCMs and thus forestall the onset of CO₂-limitation and zooxanthellae expulsion.

The new paragraph reads:

*At low to moderate levels of autotrophic disruption, it appears that the coral host may retain the capacity to utilise stored tissue (e.g. lipid) reserves and/or heterotrophic feeding (see e.g. [Borell and Bischof 2008](#)) to help maintain the CCMs and thus forestall the onset of mass zooxanthellae expulsion. However, apart from those coral species that are particularly well adapted for heterotrophic feeding, continued autotrophic disruption quickly leads to the depletion of tissue reserves ([Szmant and Gassman 1990](#); [True 2005](#)). This fact is consistent with the natural thermal bleaching sequence for a population of massive *Porites* spp. in which mass expulsion of zooxanthellae only occurred upon depletion of tissue reserves below a common lower-threshold ([True 2005](#)). A similar pre-bleaching sequence has also been noted for a branching *Acropora* spp. ([Ainsworth et al. 2008](#)). Indeed, this phenomenon may underpin empirical bleaching relationships that are characterised by specific temperature duration relationships (see e.g. [Berkelmans 2002](#)). In this case, the enhancing impact of temperature on zooxanthellae MI(%) and subsequent declines in autotrophic capacity dictate that as SSTs rise, progressively less time is required before the host's energy storage reserves fall below the level that triggers the onset of bleaching. Intuitively, this effect will be tempered by the amount of storage material maintained by the coral, and may contribute towards the explanation for why thick-tissued corals (e.g. massive *Porites* spp.) are typically more resistant to thermal stress ([Loya et al. 2001](#)). For the extreme and rapid thermal stress that characterises many laboratory experiments, mass zooxanthellae expulsion appears to precede independently of host storage reserves, and may indicate: (i) the inability of the host*

to quickly mobilise its stored energy reserves; and/or (ii) the concerted action of the coral host to re-allocate the use of its energy stores towards other homeostatic processes.

Reviewer comment #5:

(Page 4, lines 2-5) I think the concept “implications of this suggestion” pretty well summarises the fact that there is too much speculation behind the paper’s main idea. It is a valid idea that when the zooxanthellae are multiplying there is more carbon being directed into new cell production than being transferred to the host. But it is highly speculative to say that this suggestion implies that ‘the onset of the bleaching syndrome... is underpinned by the characteristic growth profile of the intracellular zooxanthellae’.

Author response #5:

This manuscript is a perspective essay, whose intent is to test/challenge the consistency of the previously proposed CO₂-limitation induced warm-water bleaching model (viz. [Wooldridge, 2009](#)); with a particular focussed attention in this case (i.e. the present article), on the importance (or not) of the demographic parameters of the algal symbionts to the proposed bleaching sequence. Thus the language “the implication of this suggestion” (and it’s like) endeavours to pick up this central tenet of the manuscript, i.e., if the CO₂-limitation bleaching model (as already outlined by [Wooldridge 2009, 2010](#)) is true (?), then there should be detectable/testable implications for the demographic parameters of the algal symbionts. From this perspective, the manuscript is then organised to show: (i) how the historical evidence is not inconsistent (i.e. does not falsify the model; despite there being alternative explanations) with these proposed implications, and (ii) how future testing could help to distinguish between the alternative explanations.

Reviewer comment #6:

(Page 4, lines 29-30) Is there a phenotypic plasticity component to this size-dependent MI relationship? Or, are there reasons to believe that each symbiont type, with its size-MI coupling, is adapted to a particular temperature and/or light habitat, which determine its distribution? Studies on the genus *Madracis* (see, e.g., Frade et al. 2008, Coral Reefs) have

raised the question whether occurring at lower densities (and larger cell sizes) is a strategy that becomes advantageous for the whole association at lower light levels. This would be an alternative explanation to why corals associating with smaller zooxanthellae (with higher MI) do bleach more often: because they are exploring an ecological niche (high light) that brings them closer to potential photosynthesis deregulation.

Author response #6:

I have previously explained (see, [Wooldridge 2010](#)) how the [Wooldridge \(2009\)](#) bleaching model predicts that each symbiont type (with its size-MI coupling) will be adapted to a particular temperature and/or light habitat, which determine its distribution. Central to this idea is the understanding that the host requires continuous photosynthate (energy) transfers from the symbiont in order to maintain a stable (and beneficial symbiosis) (sensu [Wooldridge 2010](#)). Since excessive symbiont growth and turnover can be equated with a carbon sink for the host, it follows that that reef conditions which are sub-optimal for photosynthate transfer (e.g. excessive temperature/light, or indeed low light) should favour the host's establishment of symbionts with slow intrinsic growth dynamics. Notably, coral colonies found at low-irradiance sites, whether due to depth or turbidity, are often differentially populated by the comparatively-large and slow-growing *Symbiodinium* Clade D1 (reviewed by [Stat and Gates 2011](#)). Similarly, coral colonies found at warm, shallow (excess-irradiance) sites are also often differentially populated by Clade D1 (reviewed by [Stat and Gates 2011](#)). Based on the CO₂-limitation bleaching model ([Wooldridge, 2009](#)), the well-established 'stress tolerance' associated with *Symbiodinium* Clade D1 is primarily related to its slow growth dynamic (as outlined in the present manuscript).

Reviewer comment #7:

(Page 5, lines 27-31) This information needs to be presented with respective literature sources.

Author response #7:

Agreed, have included the reference, [Dubinsky and Berman-Frank \(2001\)](#), who provide an excellent review of these concepts for the coral-algae symbiosis.

Reviewer comment #8:

(Page 6, line 12) There is a typo in the word 'photosynthate'.

Author response #8:

Agreed, and corrected.

Reviewer comment #9:

(Page 6, lines 16-28) I believe the whole discussion around C:N ratios and MI of massive vs. branching species carries significant flaws. First of all, the author "forgot" to mention that variation in C:N has also been discussed by the same cited authors as a result of different feeding rates, with the massive species studied showing a low C:N throughout all depth (Alamaru et al. 2009), characteristic of higher heterotrophic capacity. The branching species, on the other hand, showed higher C:N values in the shallow habitats. Also, when one looks at the C:N signature of the symbionts, *S. pistillata* (branching) shows a higher value than the massive *F. favus* (7.18 against 6.62 in average, respectively). This is opposed to what is reported in this review paper. Curiously, the MI values measured by Harithsa et al. (2005), unlike mentioned in this review, did not vary statistically between the massive and the branching species studied. This constitutes another important mistake! I would argue that there are also important differences between thin- and thick-tissued species in what respects light availability at the symbiont cellular level. Relevant studies reported on the enhanced skeletal multiple scattering capacity of branching species (see, e.g., Enriquez et al. 2005, *Limnology and Oceanography*) and the photoprotective role of thick tissues (see, e.g., Dimond et al. 2012, *JEMBE*), evidences that help explain why species with thick-tissues are less susceptible to bleaching than branching morphologies. This is another example in which the available literature was not properly cited and the alternative explanations available were simply ignored.

Author response #9:

Wow, there is the making of a great conspiracy story here!!! Let's try and keep some perspective. I agree (in hindsight) that the references within the discussion around C:N ratios and MI of massive vs. branching species were not well considered, but I disagree that the discussion is flawed or misleading. The key concept that I am trying to convey is that

corals harbouring zooxanthellae with high MI should correlate with lower bleaching susceptibility, and that (all-things-being-equal) zooxanthellae C:N should be a good proxy measure for the nutrient/growth status of zooxanthellae when MI data is not available (which is the most common case). In the only two studies to date where the relationship between MI and bleaching susceptibility has been directly studied/measured, it has indeed been found that the bleaching-sensitive branching and plating species have higher MI than the more bleaching-resistant massive species (see [Strychar et al. 2004](#); [Grimsditch et al. 2008](#)). For the case of zooxanthellae C:N, the results of [Cook et al. \(1994\)](#) captures well the understanding that corals with smaller zooxanthellae densities (typical of the branching-plating morphologies when compared to thick-tissued massive; [Stimson et al. 2002](#)) tend to be more replete in terms of the necessary nitrogen needed for cell replication (see Fig. 7; [Cook et al., 1994](#)). This presumably relates to the reduced competition between algae cells for the limiting supply of recycled and external nutrients. In this way, the interpretation of the MI and C:N data is consistent with the field-based conclusions of [Grimsditch et al. \(2008\)](#), who state, “our results agree with [Stimson et al.’s \(2002\)](#) findings of an inverse correlation between bleaching susceptibility and zooxanthellae density, and the conclusion that species with high densities and low MI (low zooxanthellae turnover) are more tolerant to bleaching, while species with low densities and high MI (high zooxanthellae turnover) are more susceptible.”

I have modified the revised manuscript to better reflect the key inference:

Reviewer comment #10:

(Page 7, lines 22-23) The author forgot to add that these mitotic indexes were measured during bleaching and that they can easily be a consequence, not a cause, of bleaching. Also, a particularly important observation is that at 30°C, when there is no bleaching registered, mitotic indexes also do not differ between the three species.

Author response #10:

Please check the data and read the original source (see [Strychar et al., 2004](#)). The experimental measurements were taken across the temperature range 28-32°C. No

bleaching was registered for any of the species at 28°C. Thus, how can the reviewer state that they were only measured during bleaching? Furthermore, at 30°C, the mitotic index for the branching *Acropora* sp. is ~7.0%, the *Favidae* sp. is ~5.0%), and the *Porites* sp. is ~0.7%). How can these not be different? i.e., the MI for the *Acropora* and *Porites* species differs by a factor of x10. In addition, the typical (ambient) MI for tropical symbiotic corals is ~0.1 (i.e. 1% of the zooxanthellae population; [Jones and Yellowlees 1998](#)). Thus, even for the *Porites* sp., the MI is elevated (factor x7) above ambient.

Reviewer comment #11:

(Page 7, lines 24-26) Again, here, I see there is correlation, but nowhere can a causal effect be assumed. I would, again, argue for both bleaching sensitivity and high MI being consequences.....

Author response #11:

Again, here, I would contend that my reasoning is sound and justifiable given the available evidence. This paper sets out by saying that there is a new bleaching model (viz., [Wooldridge 2009](#)), and that if it is correct, then it has implications for the demographic parameters of the symbiont population in relation to bleaching. In this paper, I review/test the validity of these implications (viz. increase MI will equate with increased bleaching sensitivity) and find them to be not invalidated by the historical evidence – despite their being alternative explanations. I do not need to speculate on the (many) other alternatives, only to confirm that the new bleaching model is not invalidated by the data – and as such, is a valid hypothesis until such time new experiments/data show it to be falsified (if indeed they can). This is how science needs to be done, so that it is not burdened down by ‘group think’.

Reviewer comment #12:

(Page 7, lines 27-29): I would like to note that [Ladriere et al. \(2008\)](#) did not compare MI of expelled vs. retained zooxanthellae for the same individuals, as the author hints. Furthermore, the study of [Baghdasarian and Muscatine \(2000\)](#) clearly states that “this pattern of cell loss can play a major role in regulating algal-cnidarian symbiosis in steady

state". That study did not study corals under bleaching conditions and there was apparently no deleterious impact of high MI on the stability of the symbiosis.

Author comment #12:

Please read the [Ladriere et al. \(2008\)](#) manuscript. The Abstract clearly states, '*Experimentally heat-shocked P. damicornis harboured, moreover, a greater number of dividing algae. Bleached individuals were found to vary as regards their response to stress, and zooxanthellae expelled from heat-shocked anemones showed a greater mitotic index....*'

For the [Baghdasarian and Muscatine \(2000\)](#) manuscript, the results are entirely consistent with the zooxanthellae growth dynamics predicted by the [Wooldridge \(2009\)](#) bleaching model - as reviewed in the present manuscript, i.e., that an increase in temperature (by raising zooxanthellae MI) will promote enhanced zooxanthellae expulsion. The [Wooldridge \(2009\)](#) bleaching model identifies the existence of a 'bleaching threshold' temperature where this enhanced turnover (i.e. growth-expulsion dynamic) represents a physiologically significant carbon sink, such that the vitally important transfer of photosynthate falls below the level needed by the host to maintain the optimal operation of the ATP-dependent carbon-concentrating mechanisms (CCM). Disruption of these CCMs is predicted to initiate CO₂-limitation and the resultant onset of (mass) zooxanthellae expulsion. That the [Baghdasarian and Muscatine \(2000\)](#) experiments did not approach the 'bleaching threshold' temperature does not change the fact that the growth-expulsion dynamic of the zooxanthellae altered in the correct fashion predicted by the [Wooldridge \(2009\)](#) bleaching model. Again, there is no contradiction here, and it appears that the reviewer has missed the key point (and motivation) of the present manuscript. I do not need to disprove all past hypotheses in order to suggest that a new one is also commensurate with the available data!!!!!!

Reviewer comment #13:

(Page 8, lines 21-22): I think what matters is the total absolute carbon translocated to the host, and not really the ratio between carbon directed to new algal cell growth vs. translocated to the host.

Author response #13:

I totally agree. But such data is rarely available, and if it is, there exists serious questions as to whether the handling and experimental procedures may have disrupted the 'typical' symbiotic cycling of carbon (and other nutrients). It is, however, well established that algal respiration (and by inference the potential amount of photosynthate available for transfer) is strongly dominated by cell division (i.e. growth).

Reviewer comment #14:

Page 8, lines 23-24: This "optimal zooxanthellae-type" concept is presented out of the context, as if the author ignores that there is a large evolutionary background determining the specificity of the symbiosis. It should at least be mentioned, somewhere along this chapter 4.2, that there is only a restricted number of genetically different symbionts that each host (from those that are capable of hosting multiple types) can establish symbiosis with.

Author response #14:

Is this 'belief' totally established for all environment conditions (pCO₂, temperature, nutrients, light). I am not convinced (as outlined in Wooldridge 2010) that there is as big a story in the concept of specificity as is currently believed. Wooldridge (2010) makes the case (and presents the supporting data) that symbiont-specific photosynthate transfer across the range of variable environmental (and colony/cellular) constraints is most likely to be the key determinant underpinning specificity. Let's let future experiments judge this one.

Reviewer comment #15:

(Page 9, line 33): Please replace "switching" with "shuffling", as the whole discussion refers to symbiont shuffling.

Author response #15:

Agreed, change to "shuffling"

Reviewer comment #16:

(Page 10, lines 11-12): It is not clear how the “superior growth dynamic of clade C symbionts” can mutually cause their preferential expulsion and later aid the displacement of another clade.

Author response #16:

Easily explained!!! With increasing temperature the superior growth dynamic of clade C is pushed past the ‘bleaching threshold’ temperature wherein enhanced clade C turnover (i.e. growth-expulsion dynamic) represents a physiologically significant carbon sink – triggering their expulsion, as mediated by the resultant onset of CO₂-limitation . So long as the slower growing clade D remain below this ‘bleaching temperature’ they will not be expelled (on mass), and thus will assume dominance. Below the ‘bleaching threshold’ temperature, the superior growth of clade C will (eventually) allow it to (again) become the dominant competitor for new host cell habitat.

It is for this reason, that the availability of nutrients (particularly nitrogen) has been explained to co-determine bleaching thresholds (see [Wooldridge and Done, 2009](#)). If nutrients are so low as to limit (constrain) cell division, then even as temperatures rise, the MI will be enforced to remain unaltered, and photosynthate transfer continue (= stable symbiosis). It is for this reason why I suggest that it is no coincidence that a unifying feature from world-wide reef locations that exhibit high (> 33°C) bleaching thresholds is their strongly oligotrophic surface waters during the warm summer months (*e.g.*, Red Sea – no summer river runoff ([Genin et al. 1995](#)), Western Pacific Warm Pool – restricted upwelling due to strong thermal stratification ([Tomczak and Godfrey, 1994](#)), Northern Australia – low nutrient loads in summer river runoff ([Wooldridge et al., 2006](#)).

Reviewer comment #17:

Chapter 5: I find this whole chapter 5 (and Fig. 6) too speculative and unnecessary.

Actually the chapter seems to be rather irrelevant for the linkage exercise the author wants to make between bleaching thresholds and the growth rate of zooxanthellae.

Author response #17:

I totally disagree, and think it is important context evidence to explain why in the present warming world, low nutrients and slow-growing symbiont types are going to become an increasingly essential feature of a stable coral-algae symbiosis. The 'cooler' temperatures over which the coral-algae symbiosis has evolved in the past helps explain why these (now) essential features were unlikely to have been as important in terms of symbiosis stability.

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