

Reviewer comment #1:

The majority of the supporting evidence cited by the author is from Symbiodinium in culture not in hospite, or from Symbiodinium in symbiosis with temperate, non-reef building coral hosts. This presents some issues in extrapolating this sparse data from a separate system into implications for bleaching in tropical reef corals.

Author response #1:

I think this concern is overstated, and cannot see how this discredits the central tenets of the paper. Temperate non-reef building corals also undergo thermal 'bleaching'. Does the reviewer suggest that a different suite of processes control 'bleaching' in temperate and tropical cnidarians symbioses?

Reviewer comment #2:

(Page 8117, Line 16) The author makes a statement about the attributes of thick and thin tissue corals, but this statement does not hold for the broader literature for either mitotic index, or C:N.

Author response #2:

I agree (in hindsight) that the references within the discussion around C:N ratios and MI of massive vs. branching species were poorly 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 (as is most often the 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 in [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 this key inference.

Reviewer comment #3:

(Section 4 and Figure 2) There is a difficulty of assigning thermal tolerance rankings in the best of data coverage, much less in a compilation of various studies from various systems and locales.

Author comment #3:

Whilst I agree, there does appear to be some generalities that are consistent across multiple studies and regions, e.g., the general higher thermal tolerance of Clade D(1) *Symbiodinium*. As highlighted in the caption of Figure 2, the thermal tolerance rankings are based on information summarised within [Steinke et al. \(2011\)](#) and [Berkelmans and van Oppen \(2006\)](#). I did not supply the rankings, i.e., they are independent of my reasoning.

Referee comment #4:

Section 4.1 A link between bleaching and MI does necessitate that Mitotic index is the driver. The high MI in the released Symbiodinium may be a consequence of a shift in state to “free-living”. As reported by (Wilkerson et al 1983 and others) mitotic index or growth rate is higher in free-living and cultured Symbiodinium than in hospite.

Author response #4:

Again, here, I would contend that my reasoning is sound and justifiable given the available evidence. This discussion paper sets out by saying that there is a new bleaching model (viz., [Wooldridge, 2009](#)), and that if it is correct, then it has testable 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 existing alternative (possibly equally plausible) explanations. I do not need to speculate on these (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 historical ‘group think’.

Referee comment #5:

(Page 8119 Lines 8-15) It is unclear what the author is positing. Is the author suggesting the corals are continuously bleaching at the edges of the colonies, and that this is driven by high mitotic index?

Author response #5:

Physiological measurements taken from zooxanthellae originating within the white tips (branching) and edges (plating) region of coral colonies demonstrate that their expulsion rates are high and continuous (see e.g., [Yamashita et al., 2011](#)) and growth rates (MI) are elevated ([Fang and Chen, 1989](#)). This physiological data (viz., visual paling, high expulsion

rates, high growth rates) is thus commensurate with the expectation of the 'boom-bust' mechanism (i.e., high zooxanthellae turnover) identified as the fundamental driver of the CO₂-limitation bleaching model (Wooldridge, 2009).

I have previously outlined how this 'boom-bust' mechanism may operate continuously in modern corals, but vary in intensity due to seasonal variations in light and temperature – thus driving seasonal changes in the upper limit of zooxanthellae biomass/density (see Wooldridge, 2009). In this way, whole-colony bleaching is the destructive end-point to a process that operates near continuously in modern corals, as alluded to by high mass transfer areas (tips and edges) in which the process dynamic is magnified - and hence evidenced (visible) even in non-bleaching years. See Wooldridge (2012), to understand why I don't think this would have been the case when atmospheric pCO₂ < 260ppm.

Cited literature

Cook, C. B, Muller-Parker, G., and Orlandini, C. D.: Ammonium enhancement of dark carbon fixation and nitrogen limitation in zooxanthellae symbiotic with reef corals *Madracis mirabilis* and *Montastrea annularis*, *Mar. Biol.*, 118, 157-165, 1994.

Grimsditch, G., Mwaura, J., Kilonzo, J., Amiyo, N., and Obura, D.: High zooxanthellae densities and turnover correlate with low bleaching tolerance in Kenyan corals, in: Ten Years After Bleaching – Facing the Consequences of Climate Change in the Indian Ocean, CORDIO Status Report 2008, CORDIO, Mombasa Kenya, 235-236, 2008.

Steinke, M., Brading, P., Kerrison, P., Warner, M. E., and Suggett, D. J.: Concentrations of dimethylsulfoniopropionate and dimethyl sulphide are strain-specific in symbiotic dinoflagellates (*Symbiodinium sp.*, Dinophyceae), *J. Phycol.*, 47, 775-783, 2011.

Stimson, J., Sakai, K., and Sembali, H.: Interspecific comparison of the symbiotic relationship in corals with high and low rates of bleaching-induced mortality, *Coral Reefs*, 21, 409-421, 2002.

Strychar, K. B., Coates, M., and Sammarco, P. W.: Loss of *Symbiodinium* from bleached Australian scleractinian corals (*Acropora hyacinthus*, *Favites complanata* and *Porites solida*), *Mar. Fresh. Res.*, 55, 135-144, 2004.

Wooldridge, S. A.: A new conceptual model for the warm-water breakdown of the coral-algae endosymbiosis, *Mar. Fresh. Res.*, 60, 483-496, 2009a.

Wooldridge, S. A.: A hypothesis linking sub-optimal seawater $p\text{CO}_2$ conditions for cnidarians-Symbiodinium symbioses with the exceedence of the interglacial threshold (>260 ppmv), *Biogeosciences*, 9, 1709-1723, 2012.