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Interactive comment on “Breakdown of the coral-algae symbiosis: towards formalising a linkage between warm-water bleaching thresholds and the growth rate of the intracellular zooxanthellae” by S. A. Wooldridge

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Review of Wooldridge, Biogeosciences Discussions, 9:8111-8139, 2012, by Ross Hill, Verena Schrameyer, Anthony W.D. Larkum, Malin Gustafsson and Peter J. Ralph

This paper provides a well-presented model for explaining warm-water bleaching in hard corals. It also attempts to use this model to explain concepts such as bleaching thresholds and symbiont shuffling. This paper is a “perspective essay” supporting “a recent hypothesis which proposes an energetic disruption to the carbon-concentrating

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mechanisms (CCMs) of the coral host, and the resultant onset of CO₂-limitation within the photosynthetic “dark reactions”, as a unifying cellular mechanism”. As such it is not expected to contain a review of all the literature. Indeed, it uses a select collection of published papers and extracts the data from these empirical studies to support the theoretical framework of this essay. This in itself is a strength of the manuscript as it highlights how a number of past studies complement each other and when considered together, allow for the construction of a new perspective on thermal bleaching in corals. However, in any such selective approach, care should be taken in reporting the findings of this research as being “parsimonious with the available evidence”. There are a number of examples of literature which do not support the findings of this study and hence the paper appears in some cases to be unbalanced and bias towards only the literature which supports a “favoured” theory.

For example, carbon-concentrating mechanisms have been found to be unaffected despite inhibition of photosynthesis (Leggat et al. 2004), and Rubisco protein content of in hospite symbionts has also been shown to remain constant during thermal bleaching, despite rapid damage to PSII (loss of D1 and PSII photochemical efficiency; Hill et al. 2011). At higher temperatures (above 36°C), Rubisco activity does rapidly drop (Leggat et al. 2004), indicating it is heat-sensitive, but likely only vulnerable to temperatures above the threshold range which induces coral bleaching. It is unclear how these significant findings can be supported by the model suggested in this paper. In the following, we will elaborate on a few points where the said ‘evidence’ does not align with the majority of with existing literature.

P 8113, L 15: care should be taken in referencing Buxton et al. 2012 (in the review mistakenly cited as 2011) in this situation as the results from this paper do not entirely support the statement. While the primary site of damage appeared to be the dark reactions in *S. pistillata*, a result also found by Jones et al. 1998 (where only *S. pistillata* tested), other coral species and various clades of cultured Symbiodinium did not show initial damage downstream of PSI in the electron transport chain. The author may,

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however, like to consider the work of Lilley et al. (2010). In addition, it is important to consider the large bodies of evidence, which suggest other locations are involved in the primary site of thermal damage.

P 8113, L 23-26: Care should be taken with a statement like this, as the author neglects to mention that the zooxanthellae can also use respirational CO₂ from the host animal, the so-called ‘internal DIC pool’ as photosynthetic substrate (Muscatine et al. 1989; Furla et al. 2000). An insufficiency in energetic substrate for active external carbon uptake does not necessarily leave the zooxanthellae in a CO₂ limiting state. Complex DIC exchanges are occurring within the holobiont and likely do not lead to CO₂ limitation (Tremblay et al. 2012).

P 8115-8118, section 3: Although this is an interesting hypothesis, it is important to remember that the nitrogen availability from the external environment to the zooxanthellae is likely not limited. Zooxanthellae of the coral *Acropora aspera* fix 14-23 times more nitrogen than their host organism as established in an DIN enrichment experiment (Pernice et al. 2012).

P8116, L 4: Corals held in elevated nutrients have also been found to have thicker tissue or more protein (Szmant 2002; Houlbrèque and Ferrier-Pagès 2009); changes which contrast to what is reported here.

P8120, L 11-12: The different MI characteristics of Symbiodinium clades are a very interesting aspect to consider in this discussion. However, it needs to be noted that there are also other stress physiological features, such as antioxidative response capacity, which differentiate Symbiodinium clades (Fisher et al. 2012). The stress response of Symbiodinium clades towards thermal bleaching are therefore different, wherefore the antioxidative pathways are more relevant to consider in the context discussed here (Downs et al. 2002; Fisher et al. 2012).

P 8120, L 15-17 and Figure 2: Assuming a general size-dependent growth relationship across Symbiodinium types should be considered with care. Several studies have

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found only small variations in growth rates between different clades under non-stress conditions (Robison and Warner, 2006; Suggett et al., 2008; Henning et al., 2009).

P 8124, L 14: How does this conclusion fit with the findings of Guest et al. (2012), who found bleaching in massive corals, while neighbouring branching corals were unbleached during a thermal event in Singapore and Malaysia? How does this present paper fit, in light of Guest et al. (2012)?

P8133, Figure 1: The direct link between reactive oxygen species (ROS) evolution and impaired photosynthesis is mentioned in the legend of Fig. 1, but nowhere discussed in the context of the paper. Given the importance of ROS in coral bleaching physiology (Lesser 1997; Perez and Weis 2006; Suggett et al. 2008), it is important to consider this in the Discussion.

Literature cited to in this review:

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