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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

Anonymous Referee #1

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General Comments

In this study the author aims at backing up the hypothesis of a linkage between the onset of bleaching in corals and the growth profile of their intracellular dinoflagellate symbionts. As a first general comment I would like to state that the question addressed is definitely relevant, that there are some interesting ideas in the paper and that these definitely deserve being tested in further experimental studies. The paper presents a novel concept, but at this moment in time, however, I do not share the author’s enthusiasm that there is enough evidence to formalise the linkage the author claims to exist.

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I think there is a general lack of hard evidence to back up the hypothesis.

On top of that, I have doubts that the manuscript serves the purpose of a review paper (in Biogeosciences) because in its present state it does not cover well the broad range of studies available in the literature about this topic. Instead of providing a thorough review of the topic of bleaching thresholds and the onset of bleaching in corals, necessarily including a non-biased selection of literature references presented in a dialectic approach to finally reach the conclusion, the author chose to present only studies that seem to support his idea. I guess the author started by elaborating an interesting concept of a mechanism to explain the onset of bleaching, and then tried to find the pieces of evidence that give support to such idea, without undertaking the necessary experiments to test it. I would say that the end result is a rather speculative, although interesting exercise that can stimulate further research but should, however, be directed to the proper channels. I believe that other authors would reach different conclusions when given the same premises, and therefore I do not consider this study as “reproducible” by other fellow scientists, even if we are talking of a review paper. As it is now, I see this as an attempt to pave the ground for a research line without actually offering the proper evidence based on hard data. Hard data can and should be collected to test this same hypothesis in a study of its own, and I strongly recommend the author to do so.

I therefore suggest that this hypothetical linkage between bleaching and symbiont growth rates should be toned down and not presented as the single most parsimonious explanation, but rather included as a very interesting hypothesis (within others) that deserves to be further tested. It is my sincere opinion that taking this new approach will reflect the available knowledge on the topic in a more accurate, responsible and comprehensive manner.

Specific comments

Before moving on to more detailed comments I would like to share some thoughts on

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the scientific rationale followed by the author.

The whole concept of the study comes about based on the observation that after an initial expulsion of the algal symbionts there is more photosynthetically fixed carbon being directed into algal cell multiplication. According to the author this suggests that under natural settings there may be a component of symbiont growth rate that is implicated on the onset of bleaching. The author argues that under increased seawater temperature (and/or high nutrients) the algal symbionts will undergo faster growth and that this causes a reduction of photosynthate flow to the host. In consequence, this reduction will then disrupt the carbon concentration mechanisms of the coral (or the nitrogen limitation state of its intracellular medium), leading to symbiont CO₂-limitation and ultimately leading to symbiont expulsion through a series of events that are downstream of those, but which are not completely explicit in this review.

To start with, please allow me putting a very naïve question... if this linkage would exist, wouldn't symbiont cell densities increase just before bleaching occurs?

In fact, the unique proposition on which this review finds its foundations, that under increased temperature there is a reduction of photosynthate flow to the host because the algal symbionts increase their growth rates, is rather weak and can have alternative explanations that were not considered by the author. Many other studies have tested and given evidence for a tight link between the disruption of photosynthesis and the onset of bleaching. Right away, a temperature-induced reduction on the translocation of glycerol and oxygen from the symbiont to the host are readily explainable by the decline in photosynthetic performance of heat-stressed algae (see, e.g., Iglesias-Prieto et al. 1992, PNAS). Several studies have shown evidence for the dysfunction of PSII under elevated temperatures, correlating with D1 protein degradation (Warner et al. 1999, PNAS), energetic uncoupling in the thylakoid membranes (Tchernov et al. 2004, PNAS), or compromised antenna protein synthesis (Takahashi et al. 2008, PNAS). This reduction in PSII activity is often accompanied by the production of reactive oxygen species, which play a role in inhibiting photosynthesis at high temperatures (Lesser

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1996, Limnology and Oceanography). This photoinhibition model of coral bleaching that is supported by many relevant studies, including recent ones (see, e.g., Hoogenboom et al. 2012, PLoS ONE), cannot possibly be ignored in such a review focusing on the onset of bleaching. Impaired symbiont photosynthesis is a commonly accepted factor determining bleaching-susceptibility and this should have been put in the right context along this review.

Besides, it is not certain that at suboptimal growth temperatures the symbionts will transfer more carbon to the host. Nowhere in the review the author presents hard evidence for this claimed increase in carbon translocation between corals and their symbionts. The author mentions that there is a higher potential for high host carbon translocation at these temperatures based on the fact that (in an isolated temperate Symbiodinium type) a lower proportion of the daily photosynthetically fixed carbon is utilised for growth (lines 15-16, page 5). However, a more logical explanation would be that under suboptimal (high) temperatures a higher proportion of the carbon is either lost by respiratory inefficiency or actually directed into protein repair (see, e.g. Robison and Warner 2006, Journal of Phycology). In the end, I would argue that for a nutrition-based symbiosis, what is decisive is not the proportion of photosynthetically fixed carbon that is being passed on to the host, but rather the absolute amounts of photosynthates. In this respect, the proposition that a higher proportion of fixed carbon becomes available for the host under (symbiont) suboptimal growth temperatures, even if realistic, is in itself not valid to justify that more carbon is actually translocated, because at these temperatures the gross carbon fixed may be substantially reduced. Therefore, to complete this rationale, I would argue that in natural circumstances, when seawater temperature increases to match symbiont optimal growth, the author's proposition does not necessarily implicate that less absolute amounts of photosynthates are being translocated to the host. However, if they do, this could as easily be attributed to the damage of the photosynthetic apparatus, and not to increased symbiont growth rates. On top of this, it is believed that tropical zooxanthellae may be tolerant to a much narrower temperature range than temperate ones (McBride et al. 2009, Journal

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of Phycology), and therefore these same premises used to build the hypothesis have firstly to be shown for tropical zooxanthellae.

Moreover, the correlation claimed to exist between bleaching thresholds and MI could as easily be explained by both parameters being a consequence of the same cause (e.g., thermal susceptibility of photosynthetic apparatus). I would rather hypothesize that symbionts living closer to their thermal threshold likely experience higher metabolic rates and/or are more exposed to photodamage and therefore need to replace their symbiont populations more often, reaching higher turnover rates, hence exhibiting higher growth rates. Following this rationale, having a high MI would be a consequence (just like bleaching is) of living under dangerous (often damaging) conditions.

For instance, the demonstrated “selfish behaviour” of some type D lineages, which have been shown to be more tolerant to bleaching and to even replace naturally occurring symbiont populations during bleaching events, is also not giving much support to the author’s idea. The fact that this symbiont prevails, after bleaching, while actually offering a lower amount of energy (photosynthates) to its host (Jones and Berkelmans 2010, PLoS ONE), represents an example against the rationale of the author.

Also, there is relevant evidence for an important role of the host in the recovery from bleaching. In fact, nowhere in the paper the author mentions heterotrophy. Hughes et al. (2010, MEPS), for instance, have shown that heterotrophically acquired carbon can be a direct source of organic carbon to the algal symbionts during bleaching. It has been also demonstrated that feeding can even prevent heated corals from bleaching (see, e.g., Ferrier-Pages et al. 2010, JEMBE). These and other studies suggest that there is a fairly more advanced interdependence between host and its symbionts than conceptualized in this review paper, and imply that a reduction of photosynthate translocation from the symbionts to the host could likely be initially compensated by the host.

I think there are substantial problems in the rather fragile piece of rationale on which

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the whole concept of this linkage between bleaching onset and symbiont growth rates is based. Therefore, again, I would suggest that more hard evidence is needed, and that the review should be focused on what we, the scientific community, actually know. I recognize the need for speculation as a means to stimulating new lines of research, but I do not think this should be the main objective of a review. I would rather like to see an experimental study presenting a hypothesis, testing it and then, yes, freely speculating on the possible mechanisms behind the findings. I would add, with all respect, that the present paper, as it is, would constitute a very interesting proposal, definitely worth of applying for research funds with. These could then be used to thoroughly test the hypothesis.

I will now present a series of detailed comments that may, or not, be related to the general comments, and which may be helpful to the author.

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

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

Page 3, lines 17-30: The listed studies and respective findings poorly represent the 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, particularly on those containing little or no hard data.

Page 3, line 28-30: I think the author needs to put in perspective the role of coral heterotrophy in bleaching susceptibility.

Page 4, line 2-5: I think the concept “implications of this suggestion” pretty well summarizes the fact 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

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ultimately underpinned by the characteristic growth profile of the intracellular zooxanthellae”.

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.

Page 5, lines 10-17: This section is thoroughly discussed above.

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

Page 6, line 12: There is a typo in the word “photosynthate”.

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.

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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.

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 30C, when there is no bleaching registered, mitotic indexes also do not differ between the three species.

Page 7, lines 24-26: Again, here, I see there is a correlation, but nowhere can a cause-effect relationship be assumed. I would, again, argue for both bleaching sensitivity and high MI being consequences of a common coral lifestyle, which probably is more dependent on autotrophy and relates to the promotion of higher intra-tissue light levels.

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.

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.

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.

Page 9, line 33: Please replace “switching” with “shuffling”, as the whole discussion refers to symbiont shuffling.

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.

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.

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