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Comment

***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 #2

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Wooldridge SA

Breakdown of the coral-algae symbiosis: towards formalising a linkage between warm-water bleaching thresholds and the growth rate of the intracellular zooxanthellae

The manuscript by Wooldridge is provocative. However, the attempt to synthesize the data into a quantitative link is not fully substantiated by broader literature. The manuscript posits that “The strength of the reviewed evidence supports a formal (quan-

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titative) linkage.” between mitotic index and bleaching. There appears to be no hard data supporting a causative role, and it is possible the link between bleaching and mitotic index may be merely an artifact of the sequence of event in the release of the symbionts. This manuscript often uses literature that does not support its case, and it ignores (or misses) literature that opposes the hypothesis. This discussion paper seems well suited to a proposal format, but requires more details on the model assumptions (not just adapted figures) and greater clarity in the connection directly linking MI to bleaching (with substantiation by data) to present a more convincing case.

The hypothesis is interesting, but this paper may benefit from simply fully outlining the hypothesis, highlighting the studies and data necessary to test this hypothesis, and the current data limitations in this area, as opposed to stating that the hypothesized model supports a quantitative linkage.

Specific Comments

Comment

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. For Example Calculations of duration of cell division come from Hoegh-Guldberg et al 1984, which in turn come from Wilkerson et al 1983, which come from a series of equations not necessarily measurements. Some of these parameters have actually not been measured in *Symbiodinium* (but estimated), and particular have not been assessed from *Symbiodinium* in corals, but other and mostly temperate cnidarian hosts. For Example Page 8115 line 22 Additionally, the MI and growth efficiencies of *Symbiodinium* (clade E) from a temperate system (Figure 3) do not represent the conditions of nutrient depleted, warmer, high light waters of the tropics. More data is necessary from reef building corals to make these statements.

Comment

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. The literature cited by the author does not support the statement made in the text. Alamaru et al 2009 has no Mitotic index data. C:N Ratios are listed for *Stylophora pistillata* (~6.9) and *Favia* (6.24).

Haristha et al 2005 does not list any C:N ratio data, and mitotic index is not significantly different between *Acropora* and *Porites*, except in a fully bleached state. Additionally, the data in the literature do not support this statement. When comparison of the broader literature is made, *Symbiodinium* from *Porites* have a higher Mitotic index (mean = 3.5) than the thin-tissue corals *Acropora* (2.8) and *Stylophora* (1.3). Also conversely to what the author states, the thicker tissue corals have similar C:N ratios as thin tissue corals. *Porites* C:N (mean = 6.3) is between that of *Acropora* (6.1) and *Pocillipora* (6.5).

There is, therefore, no logical build from statement and premise to the conclusion here and in section 5 page 8123 line 21. This weakens the whole of section 5, which does not contribute to the hypothesized model, and due to the issues with the statements, this line of reasoning should not be used to extrapolate into future conditions.

Literature for Mitotic Index *Acropora* Wilkerson, F.P. D. Kobayashi, and L. Muscatine. 1988. Mitotic index and size of symbiotic algae in Caribbean Reef corals. *Coral Reefs*. 7:29-36 Jones, R.J., and D. Yellowlees. 1997. Regulation and control of intracellular algae(=zooxanthellae) in hard corals. *Phil. Trans. R. Soc. Lond. B* 352, 457-468 Stimson, J. K. Sakai, and H. Sembali. 2002. Interspecific comparison of the symbiotic relationship in corals with high and low rates of bleaching-induced mortality. *Coral Reefs*. 21:409-421

Stylophora Wilkerson, F.P., G. Muller Parker, L. Muscatine. 1983. Temporal Patterns of Cell Division in Natural Populations of Endosymbiotic Algae, *Limnology and Oceanog-*

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raphy. 28:1009-1014 Hoegh-Guldberg, O. L.R. McCloskey, and L. Muscatine. 1987. Expulsion of Zooxanthellae by symbiotic cndarians from the Red Sea. Coral Reefs 5:201-204 Muscatine, L., P. G. Falkowski, J. W. Porter, and Z. Dubinsky. 1984. Fate of Photosynthetic Fixed Carbon in Light- and Shade-Adapted Colonies of the Symbiotic Coral *Stylophora pistillata*. Proceedings of the Royal Society of London. Series B, 222:181-202. Stimson, J. K. Sakai, and H. Sembali. 2002. Interspecific comparison of the symbiotic relationship in corals with high and low rates of bleaching-induced mortality. Coral Reefs.

Porites Gleason, D.F. 1993. Differential effects of Ultraviolet radiation on green and brown morphs of the Caribbean coral *Porites astreoides*. Limnology and Oceanography. 38:1452-1463 Stimson, J. K. Sakai, and H. Sembali. 2002. Interspecific comparison of the symbiotic relationship in corals with high and low rates of bleaching-induced mortality. Coral Reefs. Wilkerson, F.P., G. Muller Parker, L. Muscatine. 1983. Temporal Patterns of Cell Division in Natural Populations of Endosymbiotic Algae, Limnology and Oceanography. 28:1009-1014

Literature for C:N ratio

Acropora Graham, N.A.J. 2007. Ecological versatility and the decline of coral feeding fishes following climate driven coral mortality. Marine Biology 153: 119-127 Szmant, A.M., L.M. Ferrer, and L.M. FitzGerald. 1990. Nitrogen excretion and O:N ratios in reef corals: Evidence for conservation of nitrogen. Marine Biology 104:119-127

Porites Graham, N.A.J. 2007. Ecological versatility and the decline of coral feeding fishes following climate driven coral mortality. Marine Biology 153: 119-127 Schloder, C., and L. D’Croz 2004 Responses of massive and branching coral species to the combined effects of water temperature and nitrate enrichment. JEMBE 313:255-268

Pocillopora Graham, N.A.J. 2007. Ecological versatility and the decline of coral feeding fishes following climate driven coral mortality. Marine Biology 153: 119-127 Schloder, C., and L. D’Croz 2004 Responses of massive and branching coral species to the

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combined effects of water temperature and nitrate enrichment. JEMBE 313:255-268

Comment Figure 4 and description in the text appear to be an accentuation of the original work, and do not acknowledge the original statistics (Strychar et al 2004). In Wooldridge's manuscript (Figure 4), the corals are displayed as having large differences in MI%, but Strychar et al (2004) report: "There were no significant differences in MI% in any of the corals between 28 and 30°C or between 30 and 32°C (Fig 4b; $P < 0.05$, ANOVA). *Acropora hyacinthus* was the only coral to exhibit significant increases in mitotic index between 32 and 34°C ($P < 0.001$)."

Comment

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 (Steinke =3 anemones and jellyfish in culture, and one coral symbiont also in culture, with thermal tolerances reported in other studies and unpublished data; Berkelmans and van Oppen = 2 coral symbionts in hospite from the reef). In addition, as shown by Howells and coauthors (2012) the thermal tolerance of *Symbiodinium* may differ depending on local adaptation (Howells et al 2012 NCC 2:116-120). Together the variety of studies, hosts, culture conditions, and local adaptation makes broad scale statements about the thermal tolerance difficult to determine in the absence of explicit comparative data among *Symbiodinium* types.

Comment

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.

Comment

Page 8119 Lines 8-15 It is unclear what the author is positing. Is the author suggesting

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the corals are continuously bleaching at the edges of the colonies, and that this is driven by high mitotic index?

Technical Corrections

Why is the last figure listed first? Page 8118 Line 25

Grimditch spelling = Grimsditch

References

Berkelmans, R. and van Oppen, M. J. H.: The role of zooxanthellae in the thermal tolerance of corals: a “nugget of hope” for corals in an era of climate change, *P. Roy. Soc. Lond. B*, 273, 2305–2312, 2006.

Hoegh-Guldberg, O.: Population dynamics of symbiotic zooxanthellae in the coral *Pocillopora damicornis* exposed to elevated ammonium [(NH₄)₂SO₄] concentrations, *Pac. Sci.*, 48, 263–272, 1994.

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Wilkerson, F. P., Muller-Parker, G., and Muscatine, L.: Temporal patterns of cell division in natural populations of endosymbiont algae, *Limnol. Oceanogr.*, 28, 1009–1014, 1983.

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Wilkerson, F. P. D., Kobayashi, D., and Muscatine, L.: Mitotic index and size of symbiotic algae in Caribbean reef corals, *Coral Reefs*, 7, 29–36, 1988.

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