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

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Abstract

Impairment of the photosynthetic machinery of the algal endosymbiont ("zooxanthellae") is the proximal trigger for the thermal breakdown of the coral-algae symbiosis ("coral bleaching"). Yet, the primary site of thermal damage is not well resolved. In this perspective essay, I consider further a recent hypothesis which proposes an energetic disruption to the carbon-concentrating mechanisms (CCMs) of the coral host, and the resultant onset of CO_2-limitation within the photosynthetic "dark reactions", as a unifying cellular mechanism. The hypothesis identifies the enhanced retention of photosynthetic carbon for zooxanthellae (re)growth following an initial irradiance-driven expulsion event as the cause of the energetic disruption. If true, then it implies that the onset of the bleaching syndrome and setting of upper thermal bleaching limits are emergent attributes of the coral symbiosis that are ultimately underpinned by the characteristic growth profile of the intracellular zooxanthellae; which is known to depend not just on temperature, but also external (seawater) nutrient availability and zooxanthellae genotype. Here, I review this proposed bleaching linkage at a variety of observational scales, and find it to be parsimonious with the available evidence. This provides a new standpoint to consider the future prospects of the coral symbiosis in an era of rapid environmental change, including the now crucial importance of reef water quality in co-determining thermal bleaching resistance.

1 Introduction

The high productivity and extensive accretion of skeletal carbonate by shallow-water tropical reef ecosystems is testament to the evolutionary success of the symbiotic association between scleractinian ("reef-building") corals and unicellular dinoflagellate algae of the genus *Symbiodinium* ("zooxanthellae") (Fig. 7) (Veron, 1995; Stanley, 2006). Within this association, often mixed consortia of zooxanthellae types live within the coral tissues in extremely high densities (greater than 10^6 cm^{-2}) and perform intensive photosynthesis (Fig. 1a). Under the optimal conditions provided by nutrient-poor tropical waters, the vast majority ($> 90\,\%$) of this assimilated organic carbon ("photosynthate") is typically translocated to the coral, contributing substantially to its carbon and energy needs (Trench, 1993; Yellowlees et al., 2008). However, this "producer-within-consumer" arrangement is very sensitive to increases in temperature, and coral communities exposed to temperatures as little as 1–2 °C above the average summer maximum can lead to breakdown of the symbiosis. This breakdown results in expulsion of the algal partner causing the phenomenon known as coral "bleaching" (reviewed by Brown, 1997). When bleaching is severe, and the symbiosis is unable to re-establish itself, the coral host dies.

Since coral bleaching follows a decline of photosynthetic activity in the zooxanthellae within corals, impairment of photosynthesis is assumed to cause coral bleaching (Brown, 1997). Though some uncertainty remains, there is a growing body of evidence to indicate that the "dark reactions" of photosynthesis may be a primary site of thermal damage (Jones et al., 1998; Buxton et al., 2011). Recently, Wooldridge (2009a) outlined how an energy-dependent disruption to the carbon-concentrating mechanisms (CCMs) of the coral host, and the resultant onset of CO_2 limitation within the zooxanthellae "dark reactions", may provide a unifying cellular mechanism for the classic bleaching sequence of zooxanthellae photoinhibition, oxidative damage, and host cell disruption (Fig. 1b). Crucially, a tight-cycling between the cellular energy needed to activate the CCMs and the receipt of photosynthates from the zooxanthellae dictates that the zooxanthellae indirectly play a role in generating the CO_2 that they themselves require for photosynthesis (reviewed by Wooldridge, 2010). Therefore, if the flow of photosynthates from the zooxanthellae is disrupted, the capacity of the coral host to energise the CCMs could become limiting, leaving the zooxanthellae vulnerable to CO_2 limitation (and expulsion).

Wooldridge (2009a, 2010) identified the retention of photosynthate for zooxanthellae (re)growth following an initial irradiance-driven expulsion event as a likely cause of the energetic disruption to the host CCMs; i.e. when a large number of zooxathellae are expelled (per day) and then subsequently produced (per day), the increased respiratory cost of such a turnover results in a negative autotrophic balance where more carbon per day is directed into new cell production than is transferred to the coral host. The implications of this suggestion are intriguing, since it implies that in natural settings, the onset of the bleaching syndrome and setting of upper thermal bleaching limits are emergent attributes of the coral symbiosis that are ultimately underpinned by the characteristic growth profile of the intracellular zooxanthellae. Since zooxanthellae growth rates have been extensively measured, and are known to display consistent variations depending not just on temperature (Kinzie et al., 2001; Strychar et al., 2004), but also external (seawater) nutrient availability (Hoegh-Guldberg, 1994; McGuire and Szmant, 1997) and *Symbiodinium* type (Kinzie et al., 2001; Fitt, 1985), it follows that there exists a wealth of information (at a variety of observational scales) with which to test the parsimony of the proposed bleaching linkage. The following essay provides a review of this evidence, and where possible, endeavours to provide insight into the design of future experiments that can more formally test the linkage.

2 The coral-algae symbiosis: zooxanthellae cell proliferation

Dinoflagellates have relatively slow rates of cell proliferation compared to other unicellular algae (Tang, 1996). This slow growth dynamic makes zooxanthellae particularly well suited to symbiotic relationships (Wong and Kwok, 2005). In its free-living state, zooxanthellae can exist as motile zoospore (Stat et al., 2006). However, once internalised in symbio, chemical signalling by the host arrests the zooxanthellae life cycle within a cell-dividing (vegetative) non-motile state (Koike et al., 2004; Stat et al., 2006). The different zooxanthellae genotypes vary in cell size between 6–15 µm (Fig. 2), with the size of the cell directly correlating to genome size (= DNA content) (LaJeunesse et al., 2005).

The intracellular specific growth rate of the zooxanthellae (i.e. proliferation rate within the host) is estimated by measuring the proportion of algal cells undergoing cytokinesis (mitotic index, MI = the fraction of cells appearing as doublets) (Wilkerson et al., 1983). Considerable variability exists between the characteristic MI of the different zooxanthelle types. Like other forms of unicellular algae (e.g. diatoms, Geider et al., 1986) there appears to exist a general size-dependent relationship, with smaller zooxanthellae types corresponding with higher MI (Wilkerson et al., 1988). This size-dependent MI relationship may relate to the cell size dependence of DNA content (LaJeunesse et al., 2005) and/or the cell size dependence of key metabolic rates (Fitt, 1985).

Temperature also impacts upon zooxanthellae MI (Fig. 3a), with the different zooxanthellae types varying in terms of thermal growth optimum (Sakami, 2000; Kinzie et al., 2001; Strychar et al., 2004). Significantly, the thermal growth optimum for many of the zooxanthellae types that associate with corals often exceeds the thermal breakpoint of the symbiotic association (> 32 °C) (see e.g. Kinzie et al., 2001; Strychar et al., 2004). Yet, this temperature-dependent ("potential") growth rate can only be obtained when essential nutrients (particularly nitrogen) are not limiting to cell multiplication (Fitt, 2000). Persuasive evidence exists to suggest that under optimal symbiotic conditions the zooxanthellae are nitrogen-limited (Falkowski et al., 1993; Dubinsky and Jokiel, 1994; Cook et al., 1994); thereby limiting potential proliferation rates and ensuring the vitally important transfer of (excess) energy-rich photosynthates to the coral host (see next).

3 The coral-algae symbiosis: uncoupling photosynthesis from zooxanthellae growth

Carbon fixation measurements from cultured (nutrient-replete) zooxanthellae provide valuable insight into the importance of MI on the amount of photosynthate potentially available for host transfer. Figure 3b demonstrates that the optimum growth efficiency (~ 20 °C) of this *Symbiodinium* type (clade E) results in ~ 80 % of the total daily photosynthetically fixed carbon being retained for cell multiplication. However, at suboptimal growth temperatures (10 and 30 °C), growth and photosynthesis become uncoupled such that less than 11% of daily photosynthetically fixed carbon is utilised for growth; indicating the potential for high host carbon translocation at these temperatures. It is consistent that nutrient-enriched corals that harbour zooxanthellae with high MI are typically characterised by lower tissue thickness (McGuire and Szmant, 1997; Cruz-Pinon et al., 2003), reduced gamete production (Tomascik and Sander, 1987; Loya et al., 2004), and lower rates of skeletal accretion (Marubini and Davies, 1996; Ferrier-Pages et al., 2001).

The uncoupling of photosynthesis and growth in zooxanthellae is thus a necessary requirement for the continuous translocation of photosynthates to the coral host, i.e. a stable symbiosis (Dubinsky and Berman-Frank, 2001; Wooldridge, 2010). This condition is most readily achieved in oligotrophic waters that cause zooxanthellae growth rates to be nutrient-limited. In this case, the photosynthetic carbon flux of the zooxanthellae cannot be matched by the corresponding nitrogen (and phosphorus) fluxes that would be required if the zooxanthellae were to keep the carbon and use it for new cell formation. Because to increase in numbers zooxanthalle have to acquire on the order of one atom of nitrogen for every seven carbon atoms, it follows that any carbon in excess of this ratio will either be expired or translocated to the host. In corals exposed to elevated nutrient levels, the zooxanthellae, instead of acting like a carbon-moving conveyer belt translocating “energy” to the coral hosts, retain seven carbon atoms for every nitrogen atom absorbed from the water. This results in key changes in the symbiotic association. Less carbon is translocated to the host, the C : N ratios in the algae decrease (Muscatine et al., 1989), and the algae are able to use photosynthetically produced carbon skeletons for the synthesis of nitrogen-containing molecules required for cell multiplication, such as amino acids and nucleotides

The host may also contribute to maintaining the zooxanthellae nutrient-limited. Because the zooxanthellae reside with the gastrodermal cells of the coral host, any host process that removes nutrients from the intracellular milieu surrounding the zooxanthellae will act to restrict the diffusive transfer rate (i.e. cellular availability) of nutrients from the external environment. In this regard, the host tissue activity of the nitrogen-assimilating enzyme, glutamine synthetase (GS), appears particularly relevant (Yellowlees et al., 2008; Pernice et al., 2012). Significantly, the efficiency of the GS enzyme is energy (ATP) dependent. This dictates that the effectiveness of the host in maintaining the zooxanthellae growth-limited is modulated via its receipt of photosynthate; as evidenced by the significantly higher GS activity in symbiotic than in aposymbiotic animals (Wang and Douglas, 1998). In this way, any factor that disrupts the flow of photosythnate to the host (e.g. thermal bleaching) may act to release the zooxanthellae from nutrient-limitation, especially in nutrient-enriched waters. This may contribute to the reason why remnant zooxanthellae within semi-bleached hosts typically have low C : N ratios that are indicative of nitrogen-replete growth (Cook et al., 1994).

The morphological characteristics of particular coral species, which alter the path length of diffusion through coral tissue, may also constrain the supply-rate of external (seawater) nutrients for the intracellular zooxanthellae. For example, corals with thick tissues might be expected to offer greater resistance to diffusion than thin-tissue coral-types. Similarly, corals with low surface-area : volume (SA : V) morphologies (= large boundary-layer thickness) offer greater resistance to nutrient transfer than corals with diffusive (high SA : V) morphologies (Thomas and Atkinson, 1997; Baird and Atkinson, 1997). Notably, the resident zooxanthellae populations within corals with thick tissues and low SA : V (e.g. massive *Porites* spp.) have lower MI and higher C : N (both indicators of nutrient-restricted algal growth) compared with corals that have thin tissues and high SA : V (e.g. branching or plating *Acropora* spp.) (Harithsa et al., 2005; Alamaru et al., 2009). Moreover, the sites on coral colonies which display maximal rates of external nutrient transfer (e.g. tips of branching corals and the edges of plating corals (Helmuth et al., 1997) consistently have higher MI (Fang and Chen, 1989; Jones and Yellowlees, 1997).

Since both temperature and nutrients interact to co-determine the “realised” rate of zooxanthellae division, it is possible that external nutrient-enrichment need not always be detrimental to the stability of the symbiosis in cooler conditions. In this case, a low thermal (kinetic) constraint on growth, alone, may be sufficient to enforce the transfer of excess photosynthate, even from a nutrient-enlarged zooxanthellae population; thereby benefiting the host in building energy (tissue) reserves. Notably, Muller-Parker et al. (1995) found that DIN-enrichment benefited coral tissue growth during the cool winter months. High levels of DIN have also been found to support coral growth in an aquarium setting where water temperatures remain below 26 °C (Atkinson et al., 1995).

4 The coral-algae symbiosis: thermal tolerance coupled to zooxanthellae growth

To date, no experimental study has specifically targeted the impact of zooxanthellae MI on the thermal tolerance of the coral-algae symbiosis. Here, I synthesise the results from a number of related studies, which considered together, build a strong frame of reference to support a formal (quantitative) linkage.

4.1 Bleaching thresholds linked to zooxanthellae MI

Bhagooli and Hidaka (2002) found that the intracellular MI of zooxanthellae within the coral *Galaxea fasicularis* increased with temperature, and was maximal at the observed bleaching threshold temperature of 30 °C. The authors concluded that, “the host appeared to lose the capacity of controlling algal cell division after 7-day exposure to 30 °C”. A positive association between rising temperature, zooxanthellae MI, and coral bleaching was also recorded by Strychar et al. (2004) for three different coral families (*Acropora hyacinthus*, *Favites complanata* and *Porites solida*). *Porites solida* (massive morphology) was the most thermally tolerant coral, *A. hyacinthus* (branching/plate morphology) bleached most readily at low temperatures, and *F. Complanata* (mounding morphology) showed intermediate bleaching tolerance to elevated temperature (Fig. 4a). Notably, the bleaching sensitivity ranking matched the comparative intracellular zooxanthellae MI (Fig. 4b). Grimditch et al. (2008) also correlated community-level bleaching patterns with intracellular zooxanthellae MI, noting that the bleaching-sensitive branching and plating species consistently had higher MI than the more bleaching-resistant massive species.

The differential expulsion of zooxanthellae with high MI compared with those retained in the symbiosis (Baghdasarian and Muscatine, 2000; Ladriere et al., 2008) supports the deleterious impact of high zooxanthellae MI on the localised stability of the symbiosis during bleaching conditions; and may underpin the mechanism of symbiont reshuffling (see next). Individual colony bleaching patterns, which typically proceed from high mass transfer regions (tips and edges) towards low mass transfer regions (base and centre) (see e.g. Shenkar et al., 2005), also conform to the earlier explained colony-scale topology of MI. Indeed, the occurrence of "white tips" on branching corals, and "white edges" on plating corals even outside summer bleaching conditions (Oliver, 1984) may allude to the fact that whole-colony bleaching represents the destructive endpoint to a suite of cellular process that can operate near continuously in nutrient-replete coral symbioses (see e.g. Yamashita et al., 2011).

On this note, it is consistent that reef areas with high nutrient availability (whether due to terrestrial runoff or deep ocean upwelling) are characterised by lower bleaching thresholds and more severe bleaching impacts (D'Croz et al., 2001; Wooldridge, 2009b; Wooldridge and Done, 2009, Wagner et al., 2010). Indeed, a unifying feature from world-wide reef locations that exhibit high ($> 33\,^\circ$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).

4.2 Zooxanthellae reshuffling driven by preferential expulsion of zooxanthellae with high MI

As noted earlier, mass coral bleaching is consistently recorded when summer sea temperatures exceed the long-term average by 1–2 °C for more than a few days. For the cellular bleaching mechanism outlined by Wooldridge (2009a) (Fig. 1b), the dominant (initial) symbiotic response to the 1–2 °C temperature excursion is the predicted increase in MI and subsequent expulsion of zooxanthellae that are "stimulated" beyond the crucial growth dynamic (i.e. "autotrophic threshold") wherein more photosynthetically fixed carbon is dedicated to new algal cell growth than is transferred to the coral host.

The linkage of thermal bleaching thresholds to zooxanthellae MI retains relevance for the "optimal" zooxanthellae-type supported by the symbiosis under different environmental conditions. For locations that experience high summer maximum temperatures, it would clearly be advantageous for the symbiosis to be dominated by zooxanthellae that have a slow growth dynamic. On this note, it is significant that heat-tolerant clade D1 *Symbiodinium* have lower MI than heat-sensitive clade C2 *Symbiodinium* (M. J. H. van Oppen, unpublished data). A trade-off between thermal tolerance and MI has also been noted between three different *Symbiodinium* types (A6, C9b, C1) within the coral host, *Acropora intermedia* (Baird et al., 2009). Moreover, by invoking the general size-dependent growth relationship for unicellular algae, it is evident that the linkage between thermal tolerance and zooxanthellae MI may be consistent across a large number of *Symbiodinium* types (Fig 2). Indeed, even for zooxanthellae of the same genotype, size differences appear to map against thermal tolerance. For example, Howells et al. (2012) recently demonstrated that for the generalist *Symbiodinium* type C1, regionally-adapted differences in average cell diameter correlate with altered thermal tolerance; with the isolated population of physically larger (∼ 10 %) zooxanthellae maintaining greater photochemical performance and survivorship when exposed to an elevated temperature of 32 °C, both in symbiosis and in culture.

Notably, regional-scale mapping of heat-tolerant clade D1 on the Great Barrier Reef has linked its patchy occurrence (and/or the loss of more sensitive clades) to not only summer maximum temperature but also water quality (Cooper et al., 2011), particularly DIN-enrichment (Wooldridge et al., 2012b). This confirms other studies from global reef sites, which have also identified water quality as an important contributor to the enhanced occurrence of clade D1 (see e.g. Baums et al., 2010). Again, this outcome appears to identify the importance of the nutrient-dependent “realised” zooxanthella MI in explaining the “optimal” zooxanthellae partner for the prevailing thermal regime.

For corals that are capable of hosting multiple zooxanthellae types, the differential growth characteristics of the separate types may also underpin the mechanism whereby the relative abundance of the individual types dynamically alters in response to changes in environmental conditions, particularly the temperature regime (Chen et al., 2005; Berkelmans and van Oppen, 2006). In this case, the symbiotic sea anemone *Anthopleura elegantissima* presents an excellent model system to confirm the details of this “shuffling” mechanism, since it hosts both slow-growing zooxanthellae (zx) and fast-growing unicellular chlorophyte algae called zoochlorellae (zc) (McCloskey et al., 1996; Saunders and Muller-Parker, 1997). The in hospite growth rate of the smaller zc is ~ 8 times faster than the larger zx (Verde and McCloskey, 1996). The relative abundance of zx and zc within *A. elegantissima* differs along environmental gradients of light and temperature; zc predominating in cool low-light regimes and the zx predominating in warm high-light regimes (Secord and Muller-Parker, 2005). Such reshuffling is predicted by the temperature-dependent growth rates of the zc and zx. At cooler temperatures, the superior growth rate of the smaller zc allows them to competitively outgrow zx and dominate the endosymbiont population (Saunders and Muller-Parker, 1997). However, the superior growth rate of zc becomes detrimental when high midday-irradiance levels trigger excessive expulsion (McCloskey et al., 1996) and warm temperatures allow fast regrowth of the remnant zc population; this leads to the situation where more carbon per day is directed into new cell production than is transferred to the host (Verde and McCloskey, 1996). In this case, the population density of zc decreases relative to the zx population, even though the growth rate of zc is positive – even maximal (Saunders and Muller-Parker, 1997). The preferential loss of symbionts with high MI (McCloskey et al., 1996) confirms the negative selection against fast-growing symbionts during bleaching conditions, and provides the switching mechanism by which slow-growing symbionts opportunistically usurp the role as the dominant competitor.

The opportunistic shuffling between multiple symbiont partners in *A. elegantissima* appears consistent with the symbiotic functioning of the coral-zooxanthellae symbiosis. For example, the predicted slower growth dynamic of clade D (compared with clade C symbionts) supports the observations of Chen et al. (2005), who demonstrated dynamic symbiont reshuffling based on seasonal variations in temperature (Fig. 5). In this case, despite a reduction in the overall endosymbiont population size as temperature increases, clade D symbionts progressively dominate the symbiosis, as predicted by the preferential expulsion of the faster-growing clade C symbionts. However, the situation is reversed following the recovery of the endosymbiont population into the cooler winter-spring period, with the superior growth dynamic of clade C symbionts aiding the displacement of slower-growing clade D symbionts. Symbiont reshuffling based on differential growth rates may also explain observed zooxanthellae cell size (diameter) differences between semi-bleached and unbleached colonies of *Acropora Formosa* (Jones, 1997). Based on the preferential expulsion of smaller zooxanthallae (with assumed higher MI) it is consistent that the average diameter of zooxanthellae in the semi-bleached colonies was ~ 10–15 % greater than the unbleached colonies.

With this prescribed shuffling mechanism, the coral host can utilise the differential growth rates and competition that exists between zooxanthellae types (Fitt, 1985; Belda-Baillie et al., 2002) to maintain a dynamic symbiont population that is optimally matched to the prevailing conditions, particularly in terms of photosynthate delivery. This can be understood to benefit the coral host by extending the habitat range (i.e. temperature and irradiance conditions) over which it maintains photosynthate receipts from its endosymbiont population; as evidenced by the fact that shuffling from clade C2 to clade D1 symbionts facilitates a 1–1.5 °C increase in the upper thermal bleaching limit of *Acropora millepora* (Berkelmans and van Oppen, 2006). Here, the raised thermal threshold is predicted to represent the additional (permitted) level of thermal enhancement of clade D1 symbionts before they also exceed their upper “autotrophic threshold”.

5 The coral-algae symbiosis: future prospects in an era of rapid environmental change

The juxtaposition of the clocked phylogenetic tree for *Symbiodinium* with the long-term patterns in Cenozoic global climate reveals that the major diversifications in genotypes occurred during periods of global cooling and falling $p\mathrm{CO}_2$ levels (Fig. 6). Following the conceptual framework outlined in this review, it may be suggested that the progressive lowering of the constraint imposed by the "potential" thermal (kinetic) growth rate provided additional degrees of freedom for the selective envelope of the additional growth co-factors, principally defined by nutrient status, irradiance levels (depth) and zooxanthellae type. If true, it must be considered that the present ocean warming trajectory will be quickly acting to reduce those relaxed degrees of freedom such that persistence of the symbiosis necessitates that one of the other growth co-factors provides a limiting "bottleneck" to the increasing thermal growth potential. This is consistent with the fact, that present global locations which display the highest levels of bleaching resistance are united by extreme oligotrophic conditions in the warmer summer months and/or the presence of zooxanthellae types that exhibit slow intrinsic growth dynamics (e.g. clade D).

Logical extrapolation of these ideas (namely alternating relaxation and imposition of growth bottlenecks) provides the necessary functionality that is needed to explain the resilience of symbiotic corals to major climate changes over geological time, despite short-term fluctuations and losses. Furthermore, for areas that are subject to nutrient excess, the inferred capacity of thick-tissued (robust/massive) coral types and/or inability of thin-tissued (branching) coral types to provide a measure of constraint on zooxanthellae MI may explain the observed shift in community structure towards more massive morphologies (see e.g. Fabricius et al., 2005; Hennige et al., 2010). Drilling studies highlight the recent timing of this differential selection pattern for modern reefs. For example, the drilling record recovered by Aronson et al. (2004) details that for at least 2000–3000 yr prior to the last several decades, Belizean reefs were dominated by the staghorn coral *Acropora cervicornis*. The present day reefs in Belize however, have become dominated to a historically unprecedented extent by the lettuce coral *Agaricia tenuifolia*, which thrives in turbid, nutrient-enriched habitats (Shyka and Sebens, 2000). The recent demise of branching corals after long-term periods of persistence and stability has also been replicated in Florida and the Bahamas (Greenstein et al., 1998), the Caribbean (Pandolfi and Jackson, 2006), and Panama (Aronson et al., 2004). Branching species have also been differentially selected against during recent bleaching episodes throughout the Indo-Pacific (Marshall and Baird, 2000; Loya et al., 2001). Notably, coral extinction events detected in the far geological past which are linked with an excess (upwelling) supply of nutrients, also indicate the differential survival of massive or encrusting species at the expense of branching species (see e.g. Edinger and Risk, 1995). It thus appears a plausible scenario that future reef communities are likely to be increasingly dominated by massive-type growth morphologies, especially in nutrient-enriched coastal areas (Wooldridge et al., 2005).

In terms of coral reef management, it follows that local efforts to limit coastal eutrophication (and thus constrain "potential" zooxanthellae growth rates) represent a rational strategy for ameliorating climate change impacts and maintaining coral biodiversity; helping to raise the temperature thresholds that cause corals to bleach, and reducing bleaching probability across the whole range of global temperatures predicted for the 21st century (Wooldridge, 2009b; Wooldridge and Done, 2009; Wooldridge et al., 2012a).

6 Conclusions

It has long been realised that the coral-algae symbiosis is a finely tuned association, based on the "slack" between photosynthetic carbon assimilation and its retention for growth by the symbionts. In this review, much greater attention has been considered for the importance of a thermal enhancement of zooxanthellae growth, and its resultant diminution of host photosynthate transfer, in the onset of the bleaching syndrome and setting of upper thermal bleaching limits. The strength of the reviewed evidence supports a formal (quantitative) linkage. Importantly, this implies that local efforts to reduce ambient nutrient loads to reef waters, and thereby constrain “potential” zooxanthellae growth rates, represent a rational strategy for ameliorating climate change impacts on coral reefs. Future testing and refinement of the ideas presented within this paper offers considerable hope for developing further insights into tacking the climate-induced demise of coral-algae symbioses and the reefs they construct.

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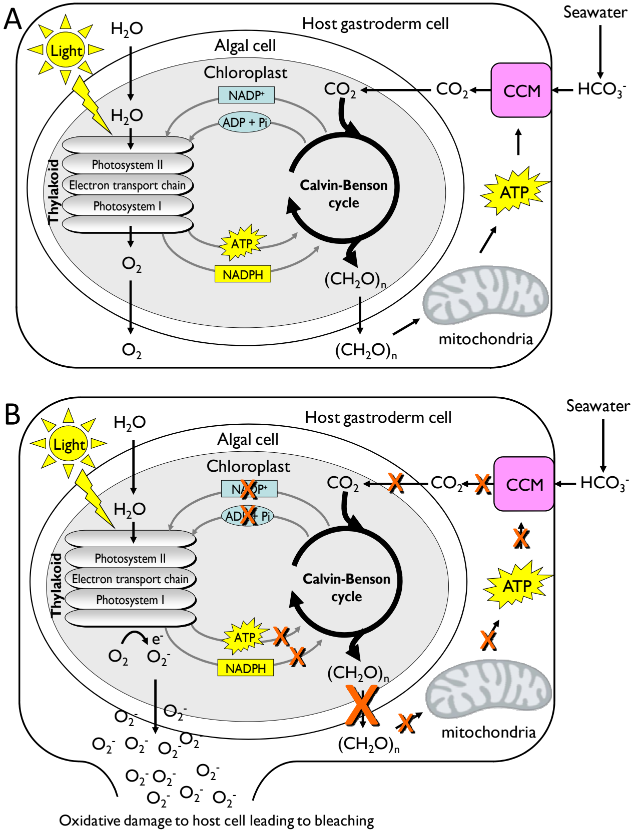

Fig. 1. The coral-algae symbiosis. **(A)** Conceptual overview of the internal carbon cycling that is maintained by the coral-zooxanthellae symbiosis (after Wooldridge, 2009a). Zooxanthellae photosynthesis takes place within the algae chloroplast, with the "light reactions" occurring in the thylakoid membranes, and the "dark reactions" (Calvin-Benson cycle) in the stroma. The vast majority (> 90 %) of the assimilated photosynthates ($(CH_2O)_N$) are typically transferred to the coral host. To ensure an adequate supply of CO_2 for its zooxanthellae, the coral host maintains a range of active CCMs. The ATP needed to activate the CCMs is ultimately derived from the transferred photosynthates. **(B)** Should the flow of photosynthates from the zooxanthellae become disrupted, then the capacity of the coral host to energise the CCMs becomes limiting, leaving the dark reaction of photosynthesis vulnerable to CO_2 (sink) limitation. With no means to turn over ATP and NADPH, the photosynthetic electron transport chain becomes blocked, which damages the light-sensitive photosystems and generates damaging reactive oxygen species that can trigger the onset of zooxanthellae expulsion (= bleaching).

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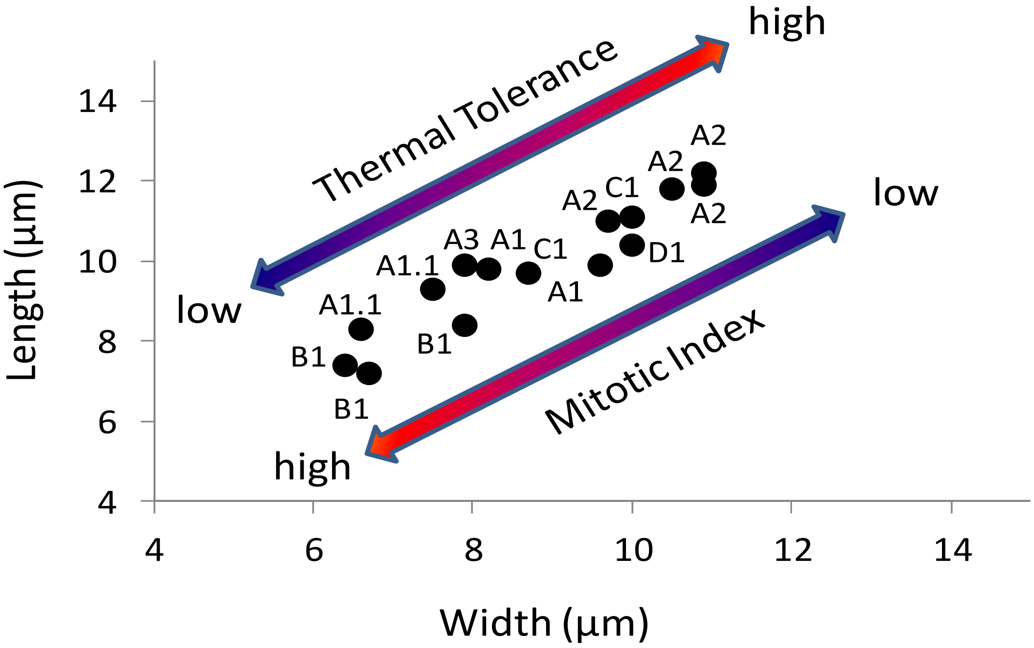

Fig. 2. Size (length and width) of dividing zooxanthellae (after LaJeunesse, 2001; LaJeunesse et al., 2005). Thermal tolerance rankings are based on information summarised within Steinke et al. (2011) and Berkelmans and van Oppen (2006). Mitotic index ranking based on generalised size-dependent relationship (after Wilkerson et al., 1988).

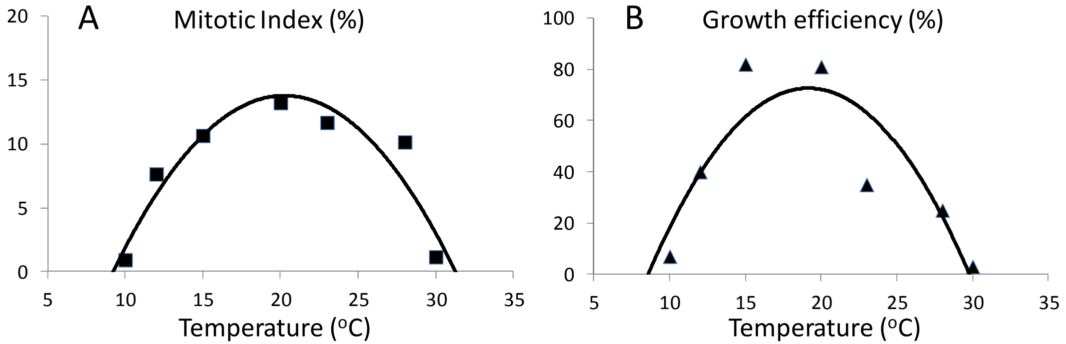

Fig. 3. *Symbiodinium californium*. **(A)** MI of *Symbiodinium californium* (in clade E) at temperatures ranging from 10 °C to 30 °C. **(B)** Corresponding carbon-based growth efficiency, i.e. percentage of daily photosynthetically fixed carbon utilized for growth (adapted from McBride et al., 2009).

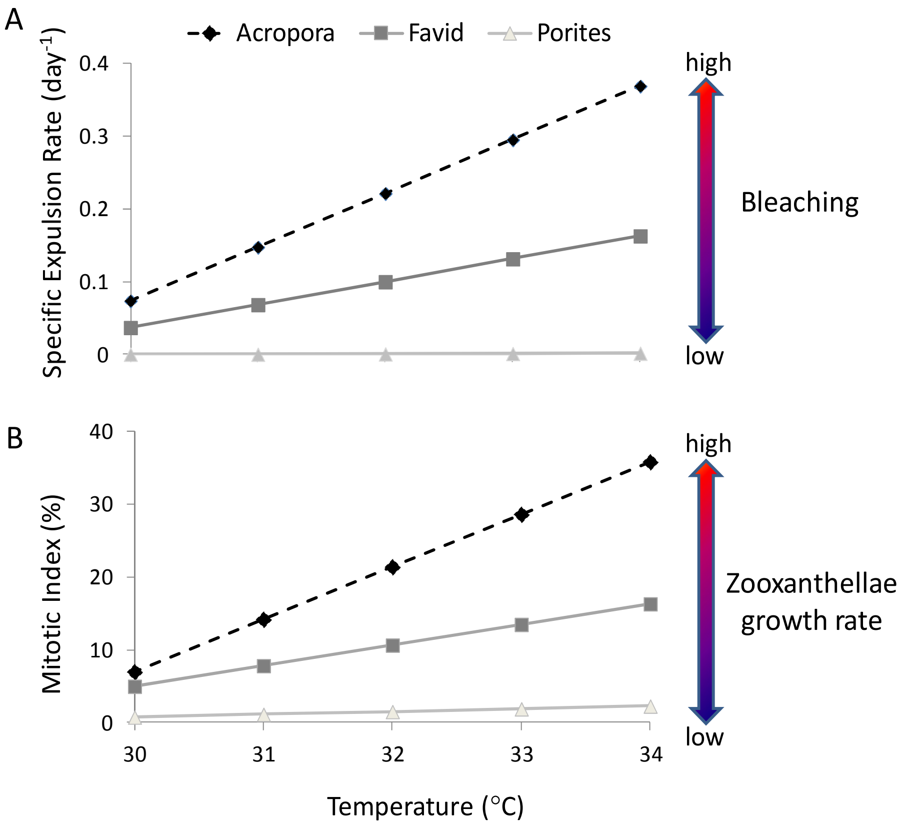

Fig. 4. *Acropora hyacinthus*, *Favites complata*, *Porites solida*. **(A)** Zooxanthellae expulsion rates (per day) for the 3 coral species. **(B)** Corresponding intracellular MI of the zooxanthellae within the 3 coral species (adapted from Strychar et al., 2004).

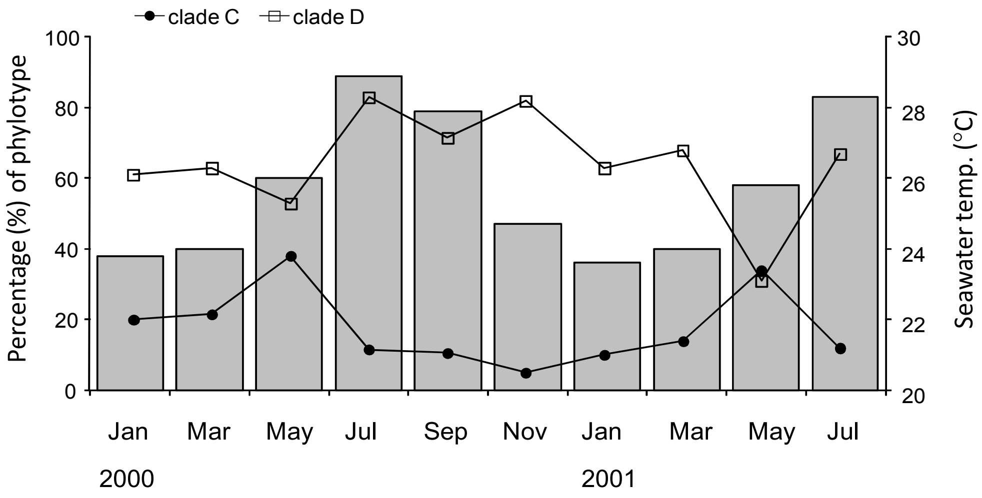

Fig. 5. *Acropora palifera*. Percentage of clade C and clade D symbionts in relation to seawater temperature and time of year (adapted from Chen et al., 2005).

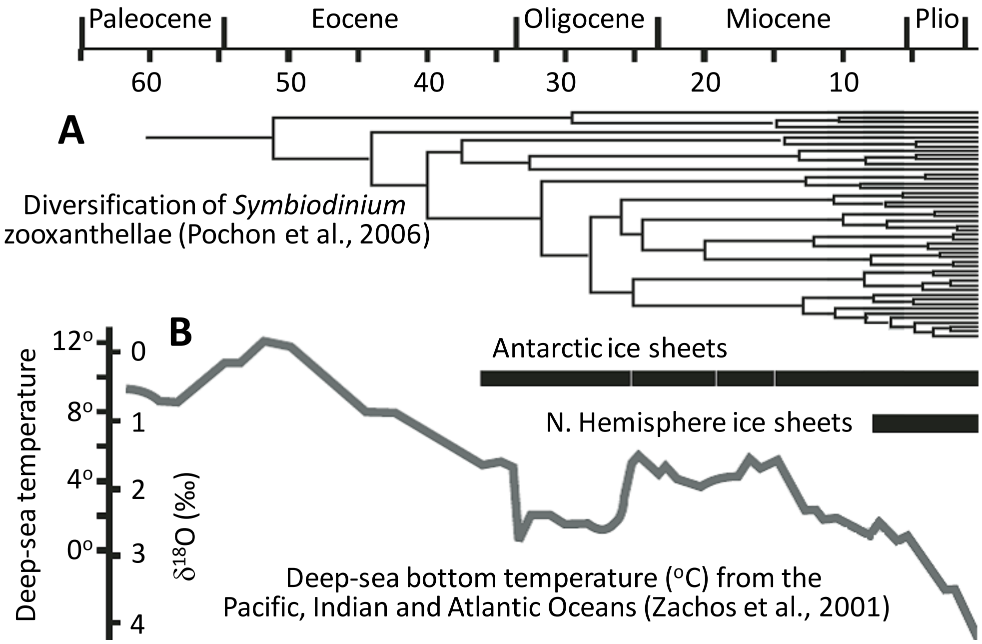

Fig. 6. Symbiodinium evolution. **(A)** Chronogram of divergence timing of symbiotic dinoflagellate *Symbiodinium* established by molecular phylogeny (Pochon et al., 2006). *Symbiodinium* originated in the early Eocene, and most extant lineages diversified after the mid-Miocene, coinciding with the last cooling that followed the mid-Miocene climate optimum. **(B)** Global deep sea oxygen record (Zachos et al., 2001) as a proxy of sea temperature changes during the Cenozoic (adapted from Pomar and Hallock, 2007).

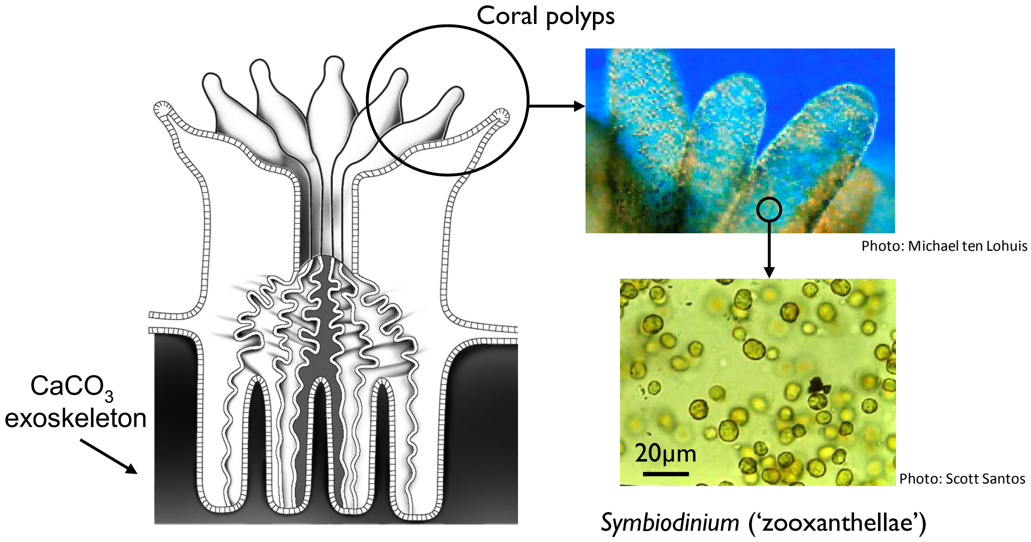

Photo: Michael ten Lohuis

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Symbiodinium (‘zooxanthellae’)

Fig. 7. A reef coral is a symbiotic association between an animal (the host) and unicellular dinoflagellate algae (the symbiont). Within this association, the dinoflagellate algae of the genus Symbiodinium (“zooxanthellae”) reside within the gastrodermal cells of the coral host. Originally it was believed that only a single zooxanthellae species engaged in the symbiotic relationship with corals. However, it is now understood that Symbiodinium are genetically diverse: consisting of eight major divergent lineages (clades A–H), with each clade containing multiple subclade genotypes (herein referred to as type(s)) (reviewed by Baker, 2003). The genetically diverse zooxanthellae types differ in their phenotypic response (e.g., growth rate, photosynthetic yield) to external conditions, particularly light and temperature regimes (Kinzie et al., 2001; Rowan, 2004). Modern genomic techniques demonstrate that many coral species can associate with multiple zooxanthellae types (often simultaneously), though the extent to which this flexibility is available to all symbiotic corals remains uncertain (Baker, 2003; Goulet, 2006).