Author Response to comment by Hill et al.

Can I first thank the reviewers for realising that this is a perspective essay, whose intent is to test/challenge the consistency of the previously proposed CO_2-limitation induced warm-water bleaching model (viz. Wooldridge, 2009); with a particular focussed attention in this case (i.e. the present article), on the importance (or not) of the demographic parameters of the algal symbionts to the proposed bleaching sequence. It is thus not, and was never intended to be an exhaustive review of all the literature on coral bleaching.

This paper contributes to previous efforts to demonstrate the consistency of the CO_2-limitation bleaching model with the considerable (but fragmented) understanding that exists for both biophysical and ecological aspects of warm-water coral bleaching. The present essay thus becomes most beneficial when considered from the fact that the proposed model has already been discussed in terms of its close alignment to the observed/predicted response characteristics arising from the well-established 'photoinhibition model' of coral bleaching (see Wooldridge, 2009); i.e., the proposed CO_2-limitation bleaching model is in complete agreement with the downstream outcomes/expectations of the photoinhibition bleaching model, which has algal photoinhibition, oxidative damage and host-cell disruption as underlying processes (Gates et al., 1992; Lesser, 1996; Jones et al., 1998; Warner et al., 1999). However, the CO_2-limitation bleaching model goes beyond the photoinhibition model to propose that in some (natural) cases, the photoinhibition response is initially triggered by a failure of the coral host to maintain a sufficient supply of CO_2 for its endosymbiont partner, particularly during periods of excess solar radiation when the photosynthetic demand for CO_2 is maximal.

As outlined by Wooldridge (2009) and summarised by Figure 1 (present paper), theoretical considerations do permit CO_2-limitation within the 'dark reactions' of photosynthesis to be proposed as a potential trigger for the classic bleaching sequence of photoinhibition, oxidative damage and zooxanthellae expulsion. In this case: (i) lack of CO_2 substrate required for the 'dark reactions' can reduce the rate of consumption of the products of photosynthetic electron transport (ATP and NADPH), subsequently causing the photosynthetic electron transport components of the 'light reactions' to become blocked (Takahashi and Murata, 2006); (ii) continued funnelling of excitation energy into the over-

reduced electron transport chain can then trigger the onset of photoinhibition (Jones and Hoegh-Guldberg, 2001), damage essential photosynthetic components, (principally photosystem II, PSII), and generate damaging reactive oxygen species (ROS) (Lesser, 1996; Warner et al., 1999); and (iii) the excess production of ROS beyond the antioxidant defence strategies of the coral host (and zooxanthellae) has been linked to the host-cell necrosis and detachment that underpins zooxanthellae expulsion (Gates et al., 1992; Dunn et al., 2002). Importantly, this sequence of events is consistent with the understanding that the bleaching process begins with impairment of the CO_2-fixation mechanism within the zooxanthellae and that the severity of the bleaching impact is a direct function of light intensity (Jones et al., 1998).

Importantly, the possibility for CO_2-limitation to be the upstream trigger of the photoinhibition response takes some of the onus off the algal photosynethic machinery (per se) as the 'weak-link' in the thermal bleaching sequence. Indeed, when viewed from the perspective provided by the CO_2-limitation model, an easily identified 'Achilles' heel' of the bleaching response is the vulnerability of the supply chain of CO_2 for the zooxanthellae; which as explained by Wooldridge (2009, 2010) and summarised in Figure 1 (present paper) is heavily reliant on a tight-cycling of autotrophic carbon/energy. It follows that any external environmental perturbation that disrupts the transfer of photosynthates to the coral host can disrupt the carbon concentrating mechanisms (CCMs) of the host, and trigger the 'bleaching' response; with the response being exacerbated in high light (= high CO_2 demand) conditions. Whilst our consideration here is thermal stress, the perturbing impact could just as equally be aerial exposure, prolonged darkness, cyanide exposure, low salinity, herbicides, pesticides, sediment smothering – all of which are known to initiate the bleaching response. Furthermore, the CO_2-limitation model has been explained to be consistent with the enhanced sensitivity to thermal stress (i.e. lower thermal thresholds) of corals exposed to nutrient enrichment (Wooldridge and Done, 2009) and pCO_2-enrichment (= ocean acidification) (Wooldridge, 2012) through their potential to excessively elevate zooxanthellae population biomass (= increased CO_2 demand).

Yet, as the present reviewers most correctly identify, it is impossible to try and validate models by anything other than attempting to falsify them (Popper, 1959). Indeed, it only requires one contradictory response to invalidate the rest. It is thus most important to

focus attention upon areas of apparent contradiction. In what is to follow, I will endeavour to resolve the areas of apparent contradiction identified by the reviewers.

Apparent contradiction #1: Respiratory CO_2 should contribute to restrict the likelihood of CO_2-limitation within the coral-algae symbiosis

Muscatine et al. (1989) explains that at low levels of solar irradiance, respiratory CO_2 arising from zooxanthellae and host metabolism is largely sufficient to meet the photosynthetic demand for CO_2. However, this contrasts with the high solar irradiance condition, when the zooxanthellae become heavily reliant on the host to supplement the internal metabolic supply with CO_2 obtained from the much larger seawater pool (Muscatine et al., 1989).

To help explain why CO_2-limitation within the coral-algae is plausible at high irradiances I provide here a quick summary of the problem and the evidence.

CO_2-limitation in alga-cnidarian symbioses

The dinoflaggelate algae (= zooxanthellae) within cnidarians symbioses utilise the Calvin–Benson cycle to fix CO_2 (Streamer et al., 1993). However, unlike other oxygenic phototrophs, zooxanthellae possess a Form II Rubisco enzyme that has a poor ability to discriminate between CO_2 and O_2 (Rowan et al., 1996). This enzymatic constraint requires that an elevated concentration of CO_2 be maintained around Rubisco to ensure continuous carbon fixation by the 'dark reactions' of photosynthesis (Leggat et al., 2002). The intracellular location of the zooxanthellae dramatically affects the source and reliability in supply of this CO_2. Muscatine et al. (1989) explained that at low levels of solar irradiance, respiratory CO_2 arising from zooxanthellae and host metabolism is largely sufficient to meet the photosynthetic demand for CO_2. This contrasts with the high solar irradiance condition, when the zooxanthellae become heavily reliant on the host to supplement the internal metabolic supply with CO_2 obtained from the much larger seawater pool (Muscatine et al., 1989). Although seawater CO_2 can freely diffuse across the lipid bilayers of the host, at typical seawater pH (8.1-8.2) it represents only a small fraction (1-2%) of the dissolved inorganic carbon (DIC) available from sea water. The much more abundant HCO_3^- (>90%),

however, is largely inhibited from diffusing into the host cells due to its ionic charge. Entry into the host cell via passive diffusion is further restricted by an unstirred boundary layer that surrounds the surface of the host, which dramatically slows the sea water–coral transfer rate for both CO_2 and HCO_3^- (Smith and Walker, 1980). For the intracellular zooxanthellae, the problem of CO_2 assimilation is thus the form of DIC and its delivery, as opposed to its availability in sea water.

It is increasingly understood that both the host and zooxanthellae have carbon concentrating mechanisms (CCMs) to help maximise the availability of CO_2 (over O_2) at the site of photosynthesis (see references in the manuscript; Goiran et al., 1996). However, these CCMs are always subject to the initial delivery constraint imposed by the presence of the unstirred boundary layer, which dramatically slows the supply rate - especially in low flow conditions. Moreover, as outlined in the manuscript, a number of the host CCMs require cellular energy in the form of ATP, which ultimately derives (over short time periods ~minutes) from the supply of fixed-carbon from the zooxanthellae. Thus, anything that restricts the photosynthetic processes of the zooxanthellae (e.g., chronic photoinhibition) can act to disrupt the efficiency of the host CCMs. This linkage of host CCMs to the tight-cycling of photosynthetic carbon is therefore an easily identified Achilles' heel in the intracellular CO_2 supply chain.

The early study of Burris et al. (1983) is commonly cited as evidence that coral zooxanthellae are not CO_2-limited. However, this study manipulated the carbonate chemistry in a very unrealistic way. Numerous other studies provide evidence that CO_2 is often in short supply at the site of photosynthesis:

- Streamer et al. (1986) suggest that a lag period in fixation of ^{14}C-bicarbonate by the branching coral *Acropora formosa* might be due to rate-limiting delivery of CO_2.
- Dennison and Barnes (1987) observed a significant increase in rates of photosynthesis and calcification in the branching coral *Acropora formosa* when surrounding water was stirred. However, when photosynthesis was near compensation, stirring had no effect, suggesting that at high rates, photosynthesis was limited by the diffusion of substrate.
- Muscatine et al. (1989) concluded from δ^{13}C values in corals that at high rates of photosynthesis, virtually all of the CO_2 that reaches the zooxanthellae is assimilated.

- Weis (1993) showed that net photosynthesis of the sea anemone *Aiptasia pulchella* was DIC-limited at present seawater concentrations (~2mM), and that photosynthesis increased up to a DIC of 5mM.
- Lesser et al. (1994) demonstrated that the coral *Pocillopora damicornis* was DIC-limited for a fixed colony morphology exposed to low flows. The data indicated that the biochemical augmentation of DIC delivery by the host/zooxanthella CCMs was unable to compensate for low flow conditions.
- Goiran et al. (1996) concluded that the zooxanthellae within the coral *Galaxea fascicularis* were DIC-limited at photosynthesis saturation, which occurred at irradiance levels of 200-300 µmol photons m^{-2} s^{-1}.
- Langdon and Atkinson (2005) showed that the net primary production from an assemblage of corals increases by 23% due to a doubling of seawater CO_2.
- Hertford et al. (2008) demonstrate for two common reef-building coral species that photosynthetic rates do not saturate until the exceedence of seawater DIC beyond 4-6mM.
- Crawely et al. (2010) demonstrate that the zooxanthellae of the branching coral *Acropora formosa* are DIC-limited at present seawater concentrations even under subsaturating (100 µmol photons m^{-2} s^{-1}) light conditions.

It is also important to keep in mind, that the majority of these studies were performed at irradiance levels that are known to maximise rates of photosynthesis (~200-300 µmol photons m^{-2} s^{-1}). However, corals in natural reef setting are frequently exposed to irradiance levels that are considerably higher than this. For example, summer irradiance levels can often exceed ~1000-1500 µmol photons m^{-2} s^{-1} for corals located in water depths less than 10m (Yentsch et al., 2002; Frade et al., 2008).

Beyond the CO_2-supply side dynamics, an increased demand for CO_2 from a nutrient-driven enlargement of the zooxanthellae population is an equally important factor in the potential onset of CO_2-limitation at the site of photosynthesis:

- Cumming and McCarty (1982) demonstrated from $\delta^{13}C$ values in corals that larger zooxanthellae populations lead to a significantly higher depletion of CO_2.

- Dubinsky et al. (1990) proposed that CO_2-limitation within the coral *Stylophora pistillata* was the most plausible explanation for the inverse correlation between zooxanthella density and photosynthesis per cell.
- Snidvongs and Kinzie (1994) used the cellular composition of in hospite zooxanthellae to propose that intracellular CO_2 was a limiting nutrient when zooxanthellae densities increase due to external nutrient additions.
- Davy and Cook (2001) proposed that the balance between zooxanthella density and CO_2 availability in the sea anemone *Aiptasia pallida* was the most likely explanation for the observed increase in photosynthetic rate per cell as the density of zooxanthellae decreased by 50% with starvation.
- Zhu et al. (2010) observed that a starvation-induced reduction in the number of zooxanthellae within the sea anemone *Stichodactyla mertensii* caused a significant increase in the photosynthetic yield of the remaining zooxanthellae, suggesting a link between CO_2 availability and the quantum yield of photochemistry in photosystem II; which is the proposed site of damage in the zooxanthellae chloroplast that triggers coral bleaching

Apparent contradiction #2: The CCM's of isolated *Symbiodinium* have been found to be unaffected despite inhibition of photosynthesis

Leggat et al. (2004) carried out experiments on isolated *Symbiodinium* and found that the algal CCM's were largely unaffected by heat stress. Whilst an interesting result, this by no means invalidates the proposed CO_2-limitation bleaching model, which has at its core the energetic disruption of the host's CCM's. As outlined by Gorain et al. (1996), both the algae and host have energy-dependent (active) CCM's.

It would seem reasonable to expect that when the extremely small (6-15 μm) isolated zooxanthellae are made available to external seawater media there would be limited chance for CO_2-limitation, except possibly in extremely high light conditions. My quick reading of Leggat et al. (2004) didn't find what irradiance levels were used in the experiment. The experiment was specifically designed to test temperature impacts.

This draws attention to another important point with proposed CO_2-limitaion bleaching model; the direct driver (trigger) is irradiance (excess CO_2 demand), whist the influence of temperature is secondary via its impact (thermal enhancement) on zooxanthellae division (growth) rates (MI(%)), which is proposed to disrupt photosynthate transfer relations and ultimately disrupt the energy-dependent host CCM's (i.e. decrease CO_2 supply). For example, expulsion of zooxanthellae owing to CO_2 limitation should only persist for as long as the demand for CO_2 exceeds the available supply. Since as a first order approximation (i.e. ignoring potential Chl-a per cell differences) the demand for CO_2 is determined by the dynamic interplay between zooxanthellae biomass and irradiance levels, a decline in either should help to return equilibrium and terminate the expulsion process. The Wooldridge (2009) bleaching model proposes that in terms of the carbon (i.e. energy) balance of the symbiosis, the MI(%) of the zooxanthellae is a crucial parameter for understanding whether the expulsion and regrowth process represents a significant carbon sink. For as long as the improved photosynthetic performance of the remaining zooxanthellae (P) (presumably now not as CO_2-limited due to decrease demand from smaller population) exceeds the respiratory cost of the regrowth and cell maintenance (R), then a net positive autotrophic carbon balance (P/R >1) may result across the diurnal irradiance cycle. The problem arises for situations in which a large number of zooxanthellae are expelled (per day) and then subsequently produced (per day). In this case, although Pmax may even remain stable, the increased respiratory cost of regrowth is predicted to lead to a negative autotrophic carbon balance (P/R <1) when integrated across the diurnal irradiance cycle. Such a situation implies a reduction or cessation in photosynthate transfer to the coral host, which may occur even when the zooxanthellae population density appears stable (= net zero growth). This inverse relationship between photosynthate transfer and symbiont MI(%) has been documented in corals (McGuire and Szmant, 1997), sea anemones (Verde and McCloskey, 1996) and jellyfish (Sachs and Wilcox, 2006).

** Just in passing, it is interesting to note that in the Leggat et al. (2004) study, even at quite extreme temperatures (>32-36^{o}C) oxygen evolution never completely ceased (i.e. photosynthesis was still continuing) in the isolated zooxanthellae (see also, Iglesias-Prieto et al., 1992). To my way of thinking, this lends support to the idea that the thermal-tolerance

of the zooxanthellae photosynthetic machinery is not the initial point of weakness leading to the bleaching syndrome. This suggestion also appears commensurate with the finding that the majority of expelled zooxanthellae from thermally stressed corals remain photosynthetically competent (Ralph et al., 2001).

*** Also, the characteristic feature of the coral bleaching syndrome is: (i) a decrease in zooxanthellae density and (ii) a decrease in Chl-a per cell of the remnant zooxanthellae. Both of these responses make sense in terms of CO_2 demand > CO_2 supply, i.e., zooxanthellae with high Chl-a per cell (= higher CO_2 demand) will be differentially selected in the expulsion sequence.

****It is reasonable to expect (as outlined in Wooldridge, 2009) that irradiance-driven competition for CO_2 may be a fundamental (homeostatic) characteristic of the coral-algae endosymbiosis, which ultimately sets the dynamic (seasonally variable) upper limit for zooxanthellae densities. The inverse relationship between zooxanthellae densities and seasonal irradiance levels is consistent with this equilibrating mechanism (Stimson 1997; Fitt *et al*. 2000). This helps makes sense of the fact that zooxanthellae expulsion occurs on a continuous (daily) basis, especially during times of high photon flux around the midday period (Stimson and Kinzie 1991; Jones and Yellowlees 1997). In this way, whole-colony bleaching can be interpreted as the destructive end-point to a process that operates near continuously in modern corals. To see why I don't think this would be the case at pCO_2 below 260 ppm read Wooldridge (2012).

***** The key inference arising from the CO_2-limitation bleaching model is that the maintenance of the coral-algae symbiosis is conditional on a continuous tight cycling of autotrophic energy, which in turn requires the algal symbionts to incur a 'fitness cost' in terms of their specific growth rate and population density. Wooldridge (2010) outlines the evidence to suggest that this fitness cost is enforced by the coral host, rather than benignly conferred by cooperating algal symbionts. Far from being unequivocally mutualistic, such symbiotic functioning is best explained in terms of a controlled parasitism whereby the coral host actively 'farms' its domesticated zooxanthellae in order to optimise the receipt of

autotrophic energy. In this way, the breakdown of the symbiosis is reposed as a breakdown in the exploitative and captive measures of the coral host.

Apparent contradiction #3: Primary site of thermal damage not within 'dark reactions' in cultured *Symbiodinium* (zooxanthellae)

The same arguments used above (viz. that CO_2-limitation is unlikely in isolated zooxanthellae) can be used here. The crucial implication of this suggestion for future coral bleaching experiments is that studies must be undertaken on the intact symbiosis and at realistic temperatures. Moreover PAM (Fv/Fm) measurements are most likely far too simplistic (integrated) to elucidate the proximal driver of the coral bleaching syndrome.

Apparent contradiction #4: Zooxanthellae growth is unlikely to nutrient (nitrogen) limited whilst in symbiosis

I think the evidence in favour of zooxanthellae being nutrient-limited is pretty strong (considered by Dubinsky and Berman-Frank, 2001), most specifically due to the fact that external nitrogen addition leads to an increase in zooxanthellae biomass (see e.g. Stimson, 1997), principally via an increase in the number of zooxanthellae per host gastrodermal cell (Muscatine et al. 1998). Based on the CO_2 arguments list above, it is easy to rationalise why corals in nutrient-replete environs may not experience an apparent increase in zooxanthellae biomass during the summer months when irradiance levels are high. The most suitable time to look would be in the lower irradiance months (winter/spring). For example, if one compares the seasonal zooxanthellae density plots from Stimson (1997) in the nutrient-enriched vs ambient seawater treatments, the zooxanthellae population is almost x2 larger in the cooler/less irradiant months, but not as different in the warm/more irradiant months.

As outlined in Wooldridge (2009, 2010), the ATP-dependent functioning of the host glutamine-synthetase (GS) enzyme dictates that the effectiveness of the host in maintaining the zooxanthellae nutrient- (growth) limited may be modulated via its receipt of autotrophic

carbon (energy), as evidenced by the significantly higher GS activity in symbiotic than in aposymbiotic animals (Wang and Douglas, 1998). Any dysfunction or 'stress' brought about by laboratory setting, or bleaching conditions may thus make it appear that the host is less efficient in restricting intracellular nutrient access to its algal partner than is reality in its natural (nutrient-depauperate) setting.

Apparent contradiction #5: Corals held in elevated nutrients often have thicker (not thinner) reserves of somatic tissue

I explain within the present paper (and Wooldridge, 2009) how this is possible (even likely), but will be conditional on cool and low irradiance conditions – most typical of the winter/spring period in low-latitude (tropical) locations. All the literature showing that nutrients have a positive influence on host tissue occurs for experimental conditions where the exposure temperatures don't exceed 26^{o}C. I believe this may help explain why the ENCORE group of experiments (Koop et al., 2001) were largely ineffective in showing a negative impact of nutrient on host physiology – as they were carried out in the comparatively cool southern region of the GBR.

Apparent contradiction #6: Different MI(%) characteristics of the *Symbiodinium* clades may not be the only physiological feature that contributes to variations in thermal tolerance

I agree. It remains critical however, that this is more fully resolved - including how these comparative factors interact with other environmental conditions/drivers (e.g., nutrient-replete vs nutrient-limited conditions). To date, zooxanthellae population dynamics have been largely ignored as an important determinant. Yet, as I have endeavoured to argue in the present manuscript, the evidence (when considered from a holistic point of view) indicates that it should not be so easily dismissed.

Apparent contradiction #7: Recent results showing massive (thick-tissued) corals were more susceptible to bleaching than neighbouring (branching) corals?

Unfortunately I have not yet read this paper, and currently cannot access in a timely fashion. I will however posit a narrative that may offer a potentially parsimonious explanation for such a response based on the resident *Symbiodinium* partner type (was it tested??). The sequence would proceed along these lines - an earlier bleaching event in the 'bleaching-sensitive' branching corals may have promoted the transition from a thermally-sensitive *Symbiodinium* type (let's say type C2) to a more thermally-tolerant *Symbiodinium* type (let's say Clade D1), leading to enhanced bleaching 'resistance'. If the thick-tissued 'bleaching-tolerant' coral hadn't experienced the earlier bleaching event it may have maintained the more sensitive *Symbiodinium* C2, thereby reducing its comparative bleaching resistant to the present event (which we may reasonably conclude was more severe than the earlier event that triggered the C2-D1 *Symbiodinium* change in the branching coral). All things being equal (i.e. the thick-tissue coral can transition the more thermally tolerant *Symbiodinium* D1-type) than it is still reasonably to expect that the thick-tissue will be the more bleaching resistant into the future. The important questions: (i) 'can all corals successfully transition different zooxanthellae types?', (ii) 'how many suitable thermally-tolerant zooxanthellae changes remain before this option becomes exhausted'??

Apparent contradiction #8: How can the known host feeding impact, which leads to enhanced bleaching resistance, be reconciled by the CO_2-limitation bleaching model?

At low to moderate levels of autotrophic disruption, it appears reasonable to suggest that the coral host may retain the capacity to utilise stored tissue (e.g. lipid) reserves and/or heterotrophic feeding (see e.g. Borell and Bischof, 2008) to help maintain the CCMs and thus forestall the onset of mass zooxanthellae expulsion (i.e. enhance bleaching resistance). However, apart from those coral species that are particularly well adapted for heterotrophic feeding, continued autotrophic disruption quickly leads to the depletion of tissue reserves (Szmant and Gassman, 1990; True, 2005). This fact is consistent with the natural thermal bleaching sequence for a population of massive *Porites* spp. in which *mass* expulsion of zooxanthellae only occurred upon depletion of tissue reserves below a common lower-

threshold (True, 2005). A similar pre-bleaching sequence has also been noted for a branching *Acropora* spp. (Ainsworth et al., 2008). Indeed, this phenomenon may underpin empirical bleaching relationships that are characterised by specific temperature duration relationships (see e.g. Berkelmans, 2002). In this case, the enhancing impact of temperature on zooxanthellae MI(%) and subsequent declines in autotrophic capacity dictate that as SSTs rise, progressively less time is required before the host's energy storage reserves fall below the level that triggers the onset of bleaching. Intuitively, this effect will be tempered by the amount of storage material maintained by the coral, and may contribute towards the explanation for why thick-tissued corals (e.g. massive *Porites* spp.) are typically more resistant to thermal stress (Loya et al., 2001). For the extreme and rapid thermal stress that characterises many laboratory experiments, mass zooxanthellae expulsion appears to precede independently of host storage reserves, and may indicate: (i) the inability of the host to quickly mobilise its stored energy reserves; and/or (ii) the concerted action of the coral host to re-allocate the use of its energy stores towards other homeostatic processes.

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