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# Differential coral bleaching—Contrasting the activity and response of enzymatic antioxidants in symbiotic partners under thermal stress



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## ABSTRACT

Mass coral bleaching due to thermal stress represents a major threat to the integrity and functioning of coral reefs. Thermal thresholds vary, however, between corals, partly as a result of the specific type of endosymbiotic dinoflagellate (Symbiodinium sp.) they harbour. The production of reactive oxygen species (ROS) in corals under thermal and light stress has been recognised as one mechanism that can lead to cellular damage and the loss of their symbiont population (Oxidative Theory of Coral Bleaching). Here, we compared the response of symbiont and host enzymatic antioxidants in the coral species Acropora millepora and Montipora digitata at 28 °C and 33 °C. A. millepora at 33 °C showed a decrease in photochemical efficiency of photosystem II (PSII) and increase in maximum midday excitation pressure on PSII, with subsequent bleaching (declining photosynthetic pigment and symbiont density). M. digitata exhibited no bleaching response and photochemical changes in its symbionts were minor. The symbiont antioxidant enzymes superoxide dismutase, ascorbate peroxidase, and catalase peroxidase showed no significant upregulation to elevated temperatures in either coral, while only catalase was significantly elevated in both coral hosts at 33 °C. Increased host catalase activity in the susceptible coral after 5 days at 33 °C was independent of antioxidant responses in the symbiont and preceded significant declines in PSII photochemical efficiencies. This finding suggests a potential decoupling of host redox mechanisms from symbiont photophysiology and raises questions about the importance of symbiont-derived ROS in initiating coral bleaching.

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#### 1. Introduction

Scleractinian corals are important ecosystem engineers building the three-dimensional coral reef framework that supports the immense biodiversity seen in tropical coastal waters. This ecological role is underpinned by the coral's endosymbiosis with dinoflagellates of the genus *Symbiodinium*, which supply carbon-rich photosynthates to the host coral, promote nitrogen recycling and conservation, and enhance

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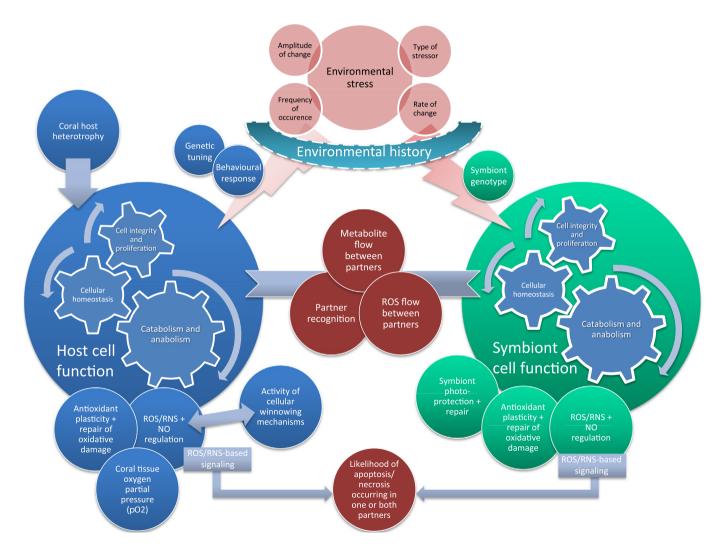
(S. Pontasch), s.dove@cms.uq.edu.au (S. Dove), oveh@uq.edu.au (O. Hoegh-Guldberg), bill.leggat@jcu.edu.au (W. Leggat), p.fisher@uq.edu.au (P.L. Fisher), simon.davy@vuw.ac.nz (S.K. Davy). rates of calcification (Muscatine and Porter, 1977). The relationship between the animal and its algal symbionts is therefore a major determinant of individual coral health and ultimately reef function. The disruption of this symbiosis by environmental stress and disease has been termed coral bleaching, since it is phenotypically visible as paling of the coral tissue as a result of a decline in symbiont photosynthetic pigment content and/or cell density (Iglesias-Prieto and Trench, 1994). With the onset of anthropogenic marine pollution and climate change, reef systems worldwide have experienced major perturbations and regime shifts, as well as bleaching events that have led to significant coral mortality (Pandolfi et al., 2003). Today, thermal bleaching triggered by ocean warming is one of the main global challenges facing reef systems.

Thermal stress thresholds and subsequent mortality vary between coral species in the reef community (Loya et al., 2001; Stimson et al., 2002). This differential bleaching susceptibility is, to a certain extent, a result of the specific holobiont composition, i.e. the combination of

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different host species and one or multiple Symbiodinium genotypes (Rowan et al., 1997; Abrego et al., 2008; Sampayo et al., 2008). In addition, physiological acclimation and repeated stress exposure (Iglesias-Prieto and Trench, 1994; Middlebrook et al., 2008; Grottoli et al., 2014), host genetic background (Smith-Keune and van Oppen, 2006; Barshis et al., 2010), symbiont effects on host physiology (Rowan, 2004; Ulstrup et al., 2007; Abrego et al., 2008), and host heterotrophy during episodes of bleaching and recovery (Grottoli et al., 2004; Grottoli et al., 2006), are important factors that define the stability and resilience of the coral symbiosis (Fig. 1). However, the relative importance of different symbionts to the holobiont's resilience is difficult to assess due to complex interactions and trade-offs (Fitt et al., 2001; Abrego et al., 2008; Fitt et al., 2009; Jones and Berkelmans, 2010). Moreover, while some intracellular sites and effects of thermal damage in the host and symbiont have been identified, there is no consensus about the causal chain of events and the supposed 'weak link' in the symbiosis. Indeed, bleaching can be manifested as host-cell detachment and/or release of potentially photosynthetically competent symbionts (Gates et al., 1992; Ralph et al., 2001), as well as breakdown of photosynthetic dark and light reactions (Jones et al., 1998; Warner et al., 1999), and apoptosis and necrosis in both partners (Dunn et al., 2004; Tchernov et al., 2011; Hawkins et al., 2013; Paxton et al., 2013).

One key process, first suggested by Lesser et al. (1990), is the leakage of reactive oxygen species (ROS) from the symbiont to the host, which then challenges and potentially overwhelms the host's antioxidant capacity under stressful conditions (Downs et al., 2002; Weis, 2008). In addition, high levels of ROS as well as reactive nitrogen species (RNS) in the host gastrodermal cell could stimulate innate immune-like pathways and potentially trigger pro-apoptotic processes in the host (Fig. 1, Perez and Weis, 2006; Dunn et al., 2007; Hawkins et al., 2013). The involvement of ROS in coral bleaching led to the proposal of a unifying mechanistic model of coral bleaching: the 'Oxidative Theory of Coral Bleaching' (OTB). This hypothesis proposes that exposure to temperature and light stress initiates the bleaching cascade primarily by compromising symbiont photosynthesis, leading to the excessive generation of ROS and RNS in the symbiont (reviewed in Weis, 2008). Potential ROS leakage into the host tissue in combination with damage and possible activation of apoptotic pathways in both partners results in the breakdown of the symbiotic relationship (reviewed in Weis, 2008; Lesser, 2011).



**Fig. 1.** *The dynamics associated with coral health under stress.* Conceptual diagram of key physiological elements that contribute to differential coral bleaching susceptibility under stress. Maintaining cellular functioning under stress is essential to the maintenance of the mutualistic association, because cellular stress directly influences the relationship between coral host and dinoflagellate symbionts with regard to partner recognition, metabolite flow, and ROS flow. Mechanisms related to repair and prevention of oxidative damage play a key role since they determine the threshold for oxidative stress-induced cell death (necrotic or apoptotic) in both partners and potentially also influence host-symbiont recognition. The particular bleaching pathology of the holobiont and the primary impact sites (e.g., host vs. symbiont) are dependent on the specific nature of the stressor and its properties (e.g., heating rate of thermal stress). The particular impact of stress is furthermore modulated by the environmental history of the holobiont as well as specific behavioural responses (e.g., host tissue retraction under high light stress) or genetic factors. This conceptual diagram is not intended to be complete—placing its primary focus on the role of oxidative stress-related mechanisms and their connection to other physiological processes. ROS, reactive oxygen species; RNS reactive nitrogen species; NO nitric oxide.

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