

NOTE

A new conceptual model for the enhanced release of mucus in symbiotic reef corals during 'bleaching' conditions

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ABSTRACT: Symbiotic reef corals exude large volumes of mucus when exposed to environmental conditions that challenge the integrity of the coral-algae endosymbiosis. Here, the physiological consequences of CO₂-limitation within the 'dark' photosynthetic reactions of the algal endosymbionts ('zooxanthellae') are investigated as the possible cause of the release of 2 different forms of mucus: mucus-polysaccharide and mucus-lipid. This mechanism may explain why the experimental addition of specific host-derived free amino acids (commonly referred to as 'host factors') enhances photosynthate release and carbon fixation rates from *in vitro* zooxanthellae. Furthermore, it reinforces the often-ignored importance of the coral host in maintaining the stability and functioning of the intact symbiosis in the face of environmental stress, even supporting the possibility that disruption to host-controlled processes ultimately triggers the breakdown of the symbiosis leading to the mass expulsion of zooxanthellae ('coral bleaching').

KEY WORDS: Coral bleaching · Host release factor · Photoinhibition · Lipogenesis

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INTRODUCTION

In favourable environmental conditions, the symbiosis between corals and dinoflagellate algae of the genus *Symbiodinium* ('zooxanthellae') is characterised by a translocation of excess fixed-carbon photosynthetic products ('photosynthates') from the zooxanthellae to the coral host (Fig. 1a; Trench 1993). This ready supply of energy-rich photosynthate benefits the coral host by fuelling its production of tissues, skeleton and gametes. Indicative of these physiological benefits, the coral host maintains a range of homeostatic strategies to maximise its receipt of photosynthate. This includes 'CO₂-concentrating mechanisms' (CCMs) that enhance the intracellular supply of CO_{2(aq)} needed for intensive zooxanthellae photosynthesis (Weis et al. 1989, Goiran et al. 1996, Leggat et al. 2002). It has also been speculated that the diversion of photosynthate away from zooxanthellae metabolism towards release

is stimulated by putative 'host factor' signalling molecules (Gates et al. 1995, Wang & Douglas 1997).

Given these active host strategies, it is a surprising (enigmatic) characteristic of the intact symbiosis that a significant proportion of the net carbon assimilated by zooxanthellae is simply released as exudates, including coral mucus. For example, mucus release has often been reported to constitute ~50% of the daily carbon balance in shallow-water reef corals (Crossland et al. 1980, Davies 1984), though at certain times this value can be much higher (e.g. ~98%; Ikeda & Miyachi 1995). Whilst a role for mucus has been assigned to a variety of homeostatic processes (e.g. a release mechanism for excess assimilated carbon, desiccation resistance, defence against pathogens, feeding, sediment cleaning), the current understanding of the composition, production and symbiotic function of mucus remains fragmentary (reviewed by Brown & Bythell 2005). One aspect of coral mucus production that has

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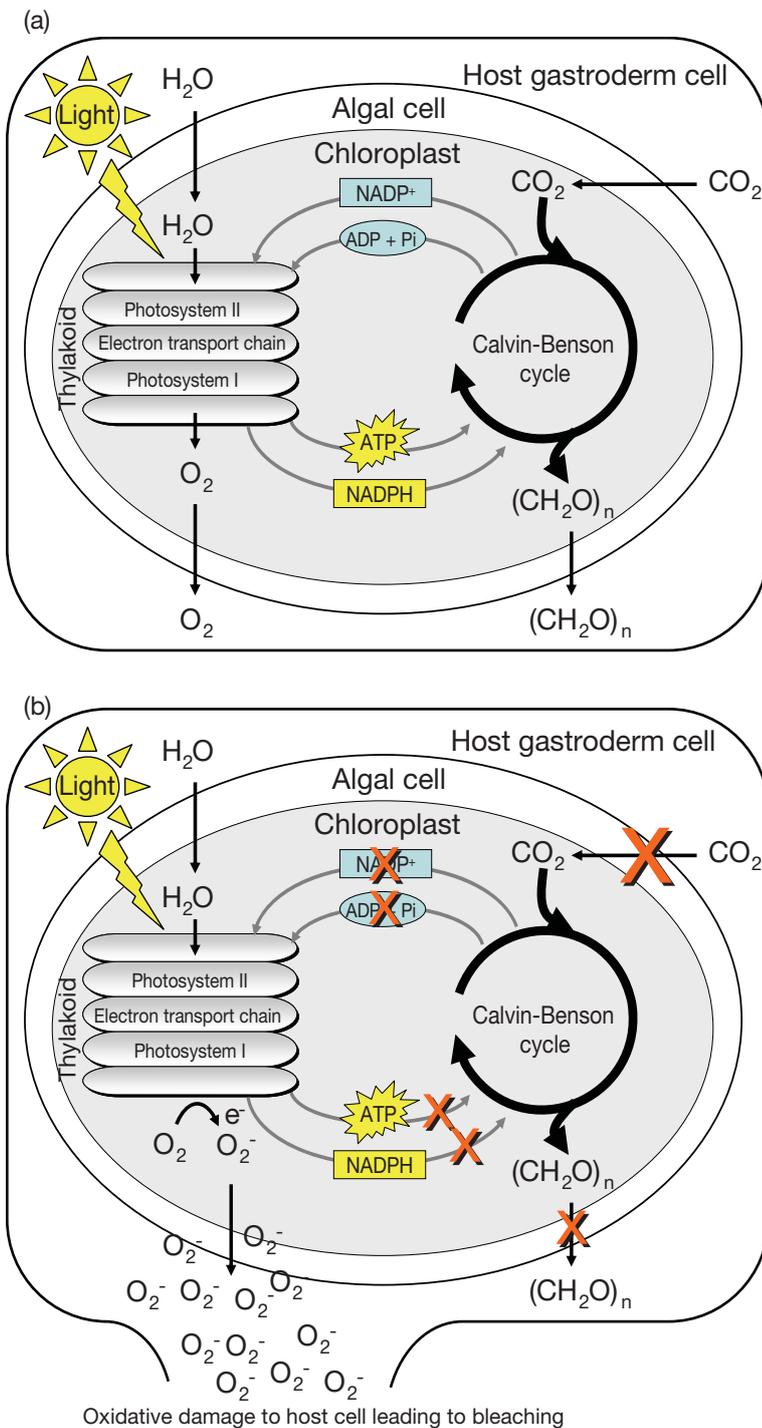


Fig. 1. (a) Conceptual overview of the internal carbon cycling that is maintained by the coral-zooxanthellae symbiosis. Zooxanthellae photosynthesis takes place within the algal chloroplast, with the 'light' reactions occurring in the thylakoid membranes and the 'dark' reactions (Calvin-Benson cycle) in the stroma. (b) Conceptual representation of the breakdown of the symbiosis (= zooxanthellae expulsion), as triggered by a limitation of CO_{2(aq)} substrate for the 'dark' reactions of zooxanthellae photosynthesis (after Wooldridge 2009). 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

received only limited consideration is its strong relationship to the breakdown of the coral-algae association, in which the zooxanthellae are released en masse ('coral bleaching') (Fig. 2; Kato 1987). Indeed, enhanced mucus release is associated with many known bleaching risk factors, including heat stress (Neudecker 1983, Kato 1987), cold stress (Steen & Muscatine 1987, Saxby et al. 2003), aerial exposure (Krupp 1984, Kato 1987, Romaine et al. 1997), low flow (Coffroth 1985, 1988), salinity stress (Coffroth 1985, Kato 1987, van Woesik et al. 1995), excess solar radiation (Drollet et al. 1993, 1997), excessive sedimentation (Coffroth 1985), cyanide exposure (Cervino et al. 2003), or herbicide exposure (Jones & Kerswell 2003).

Whilst the environmental triggers of coral bleaching (and associated mucus secretion response) are self-evident, uncertainty surrounds the cellular (symbiotic) conditions underpinning the bleaching syndrome. Recently, Wooldridge (2009) identified the onset of CO₂-limitation within the 'dark' reactions of zooxanthellae photosynthesis as a potential unifying cellular mechanism (trigger) for the classic bleaching sequence of zooxanthellae photoinhibition, oxidative damage, and host cell disruption (Fig. 1b). In this case, (1) lack of CO_{2(aq)} substrate required for the 'dark' reactions restricts the consumption of 'light' reaction products (ATP and NADPH), which blocks the photosynthetic electron transport chain (= sink-limitation) (Takahashi & Murata 2006); (2) continued funnelling of excitation energy into the over-reduced electron transport chain triggers the onset of photoinhibition (Jones & Hoegh-Guldberg 2001), which damages essential photosynthetic components (principally photosystem II, PSII), and generates damaging reactive oxygen species (ROS) (Lesser 1996, Warner et al. 1999); and (3) the excess production of ROS beyond the antioxidant defence strategies of the coral host (and zooxanthellae) initiates the host cell necrosis and apoptosis that underpins zooxanthellae expulsion (Gates et al. 1992, Dunn et al. 2002).

This scheme is consistent with light flux being an important co-determinant of the severity of the bleaching response, since ultraviolet radiation (UVR) contributes direct damage to PSII (Nishiyama et al. 2006),

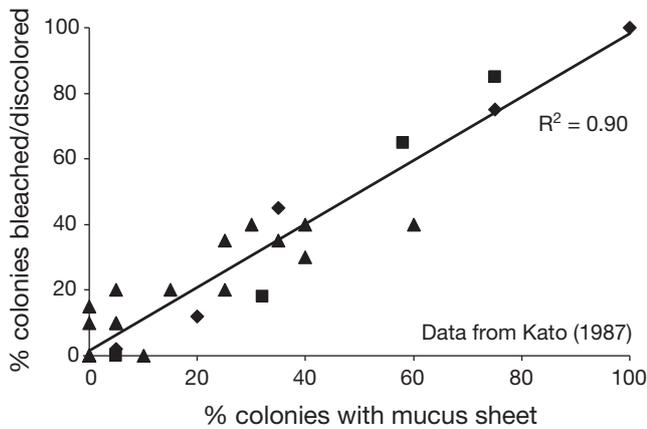


Fig. 2. *Porites cylindrica*. Mucus secretion and coral bleaching in a reef-building coral (after Kato 1987). The mucus-bleaching data include field observations for a natural thermal bleaching event (▲), and laboratory responses that resulted from various levels of thermal stress (◆) and salinity stress (■)

whilst periods of excess photosynthetic active radiation (PAR) (= high photosynthetic demand for CO₂) can trigger the onset of CO₂-limiting conditions within the intracellular zooxanthellae population (Muscatine et al. 1989). Environmentally driven breakdown of the host CCMs may also trigger CO₂-limitation via a disruption in the supply of intracellular CO₂ (Wooldridge 2009, Wooldridge & Done 2009). Importantly, the CO₂-limitation bleaching model identifies the potential for zooxanthellae expulsion to occur on an almost continuous (daily) basis, which is consistent with experimental observations of daily zooxanthellae release, especially during times of high photon flux around the midday period (Stimson & Kinzie 1991, Jones & Yellowlees 1997).

In this article, I utilise the CO₂-limitation bleaching model as an instructive standpoint from which to develop a new conceptual interpretation (model) for the enhanced release of mucus in symbiotic reef corals during 'bleaching' conditions. Whilst no new data sets are introduced, new inference is drawn by reconsidering (testing) existing observations from the identified scenario of CO₂-limitation within the 'dark' reactions of photosynthesis during periods of excess solar irradiance (sensu Wooldridge 2009). The new interpretation delivers 2 contrasting endpoints: (1) increased mucus excretion as a host strategy to limit the onset (and consequences) of photoinhibition in its zooxanthellae population, and/or (2) mucus excretion as a deleterious consequence of host cell membrane disruption associated with zooxanthellae photodamage. These alternate outcomes are explained in terms of 2 different forms of mucus: mucus-polysaccharide and mucus-lipid.

MUCUS RELEASE AS A PHOTOPROTECTIVE MECHANISM

Mucus-polysaccharide is a gel-like organic exudate associated with specialized mucus-producing cells (i.e. mucocytes) that are primarily located in the oral epithelium of the coral host (reviewed by Brown & Bythell 2005). Though still requiring further experimental verification, it is commonly believed that mucocytes convert free lipid droplets stored within the host cytoplasm into mucus-polysaccharides, which are then secreted onto the surface of the coral (Fig. 3; Brown & Bythell 2005). The presence of UVR-absorbing mycosporine-like amino acids (MAAs) in the surface-covering exudate (Drollet et al. 1993, 1997) draws attention to the role of mucus-polysaccharides in protecting (screening) the coral and their zooxanthellae from the deleterious physiological impacts of excessive solar irradiance. This inference is strengthened by the observation that maximal release of mucus-polysaccharides coincides with the midday-peak in the diurnal irradiance cycle (Fig. 4; Crossland et al. 1980, Crossland 1987). It remains to be tested whether mucus-polysaccharides also attenuate (i.e. absorb and/or scatter) PAR and thereby help to limit the deleterious CO₂-limitation bleaching sequence. It appears relevant that mucus-polysaccharide secretion is most common during periods when the coral polyps are retracted (Coffroth 1988). Daytime polyp retraction lowers the intensity of PAR reaching the endosymbiont population (Salih et al. 2000, Brown et al. 2002); there-

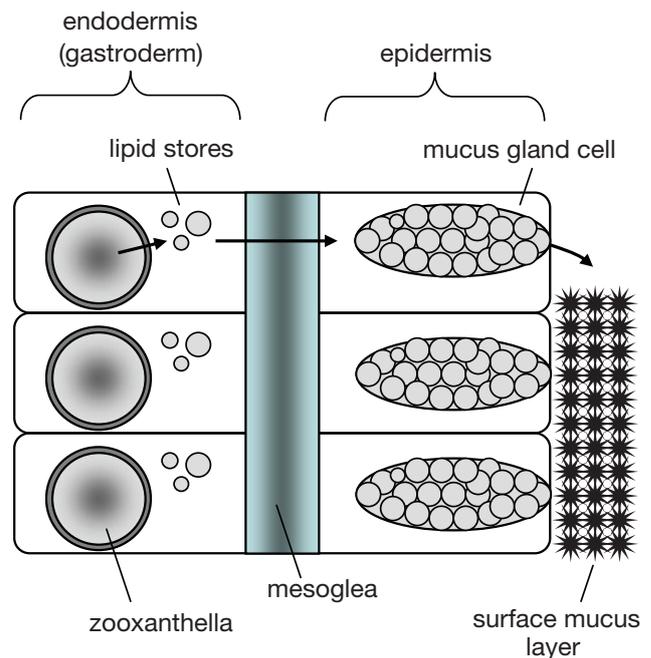


Fig. 3. Proposed cellular sequence leading to the surface secretion of mucus-polysaccharide (adapted from Brown & Bythell 2005)

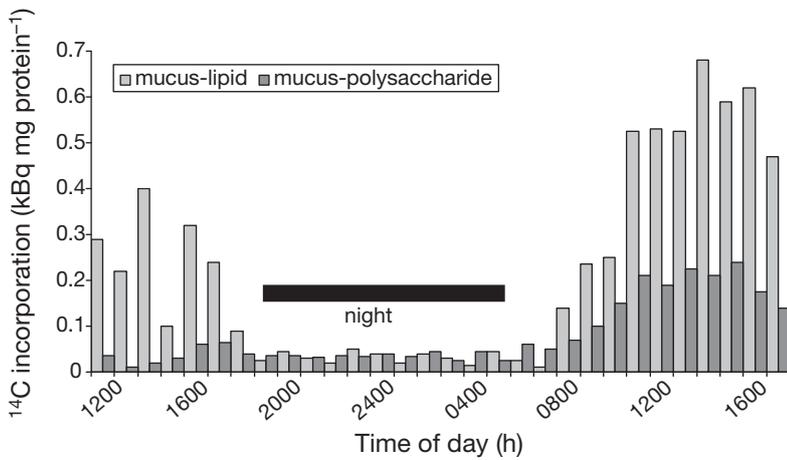


Fig. 4. *Acropora acuminata*. Diurnal variation in the incorporation rate of labelled ¹⁴C into mucus-polysaccharide and mucus-lipid (after Crossland et al. 1980)

fore, its association with the release of mucus-polysaccharides fits with the notion that the coral host actively seeks to moderate the midday photon flux entering the photosynthetic apparatus of its zooxanthellae—thereby effectively lowering the maximum instantaneous (endpoint) demand for CO_{2(aq)} within the ‘dark’ photosynthetic reactions. Production of fluorescent pigments (FPs) that dissipate excess light energy via fluorescence and light scattering (Salih et al. 2000) is an additional (consistent) host-dependent photoprotection strategy.

Beyond the solar screening role, the lipid synthesis process that supports mucus-polysaccharide secretion may also confer photoprotection during periods when the ‘dark’ reactions of photosynthesis are CO₂-limited. For this proposed ‘bleaching’ condition (Fig. 1b), lipid synthesis within the chloroplasts of zooxanthellae may still be achieved provided that carbon products (e.g. acetate) are transferred from the host to the zooxanthellae (Fig. 5; Patton et al. 1977, Blanquet et al. 1979). In this scheme, zooxanthellae absorb acetate which is produced by breakdown of lipids and/or digestive and degradative protein metabolism (‘amino acid catabolism’) in the host cell. Once inside the zooxanthellae, the acetate molecules are activated and converted to fatty acids, using excess ATP and NADPH to power the energetically costly process; one molecule of ATP and 2 molecules of NADPH are required for the addition of each 2-carbon (acetate) unit. The zooxan-

thellae then transfer the carbon back to the host as newly synthesized lipids, typically as a form of wax ester or triacylglycerol. By providing an alternative sink for excess ATP and NADPH, this process can be understood to help forestall over-reduction of the photosynthetic electron transport chain, thereby reducing the potential for photoinhibition, oxidative damage and zooxanthellae expulsion.

Support for the operation of this photoprotective mechanism is found in the biophysical and biochemical responses (host cellular cues) that accompany the bleaching process. For example, in the early stages of thermal bleaching in *Montastraea annularis* there is a dynamic (adaptive) increase in the abundance of mucocytes in the oral epidermal tissue layer

(Piggot et al. 2009). Moreover, during the early stages of thermal bleaching in *M. franski*, host gastroderm cells containing zooxanthellae become progressively enriched with free amino acids (FAAs) and lipid products (Edmunds et al. 1995, Gates & Edmunds 1999). A similar result has been recorded for the reef-building coral *Pocillopora damicornis*, wherein the early stages of thermal bleaching are associated with an enhanced presence of lipid globules within host gastroderm cells and associated zooxanthellae (Salih et al. 1998). In this case, lipid globules were observed to protrude (‘bleb’) from the surface of the zooxanthellae. Consistent with the lipid synthesis/CO₂-limitation alleviation strategy

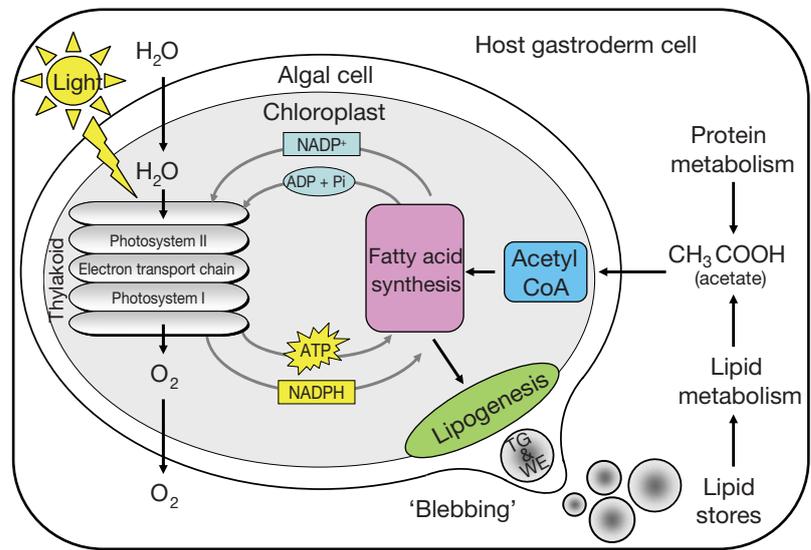


Fig. 5. Proposed cellular pathways by which the host recycles acetate, and by which lipid droplets are synthesized and secreted by symbiotic zooxanthellae (adapted from Kellogg & Patton 1983). TG: triacylglycerol, WE: Wax ester

outlined here, the quantity of lipid globules within the zooxanthellae showed a strong interaction with PAR, with the highest number of lipid globules present for the combined high PAR and temperature treatment, followed by the high PAR alone treatment—both treatments showing a dramatic increase compared to dark or shaded treatments.

The postulated involvement of zooxanthellae processes with the release of coral mucus is consistent with previous studies which have detected significant amounts (up to 47 mol%) of arabinose in coral mucus (Ducklow & Mitchell 1979, Meikle et al. 1988). Arabinose is not a common constituent of animal cells, suggesting the likely involvement of the zooxanthellae, as it is a universal constituent of plants.

MUCUS RELEASE AS AN INDICATOR OF HOST CELL DISRUPTION

Coincident with the midday-maximum secretion of mucus-polysaccharide is the release of a liquid mucus-lipid (Fig. 4; Crossland et al. 1980, Crossland 1987). In fact, the release rate of mucus-lipid represents about 3 to 4 times that of mucus-polysaccharide (Crossland 1987). From the discussions above, it is evident that periods of excess irradiance which promote the bleaching syndrome can cause the host gastroderm cells (in which the zooxanthellae reside) to become temporarily enriched in mucus-lipids. Photooxidative damage, leading to the disruption in the integrity of the host cell membranes (Gates et al. 1992), can trigger the release of this mucus-lipid material together with (healthy and degraded) zooxanthellae. For example, histological observations by Hayes & Bush (1990) confirm that during the thermal bleaching of the symbiotic reef coral *Montastraea annularis*, disruption to the cellular integrity of the oral gastroderm causes the release of zooxanthellae and mucus-lipid into the gastrovascular cavity. Similar histological observations have been noted for other bleaching stress factors, such as reduced salinity (van Woesik et al. 1995), cold stress (Steen & Muscatine 1987) and cyanide exposure (Cervino et al. 2003). Implicit with such a mechanism is the release of mucus-lipid and zooxanthellae from out of the coelenteral mouth of the coral host, as opposed to the mucocyte cells in the case of mucus-polysaccharides. In this respect, it is noteworthy that several *Faviid* spp. have been observed 'streaming' mucus material through their mouth (detailed in Brown & Bythell 2005). Indeed, the potential correspondence of this process with the well-described (daily) coelenteral release of mucus accumulations ('pellets') containing both degraded and healthy zooxanthellae (see e.g. Steele 1977, Titlyanov et al. 1996) deserves further attention.

DISCUSSION

The extensive and continuous (daily) release of mucus from symbiotic reef corals, particularly around the peak-midday irradiance period, has most often been cited as an inevitable consequence (byproduct) of phototrophic nutrition, i.e. since the energy-rich (but nitrogen-poor) algal photosynthate cannot itself support animal tissue growth, the coral host is compelled to excrete excess photosynthate that is surplus to its respiratory requirements (see e.g. Davies 1984, Dubinsky & Jokiel 1994). Yet, this explanation has no basis during bleaching conditions when respiration rates (R) exceed photosynthesis (P) (i.e. $P/R < 1$; Coles & Jokiel 1977, Al-Horani 2005) and host energy stores become progressively depleted (Yamashiro et al. 2005, Anthony et al. 2007). Furthermore, it cannot explain the enhanced presence of lipid globules within the gastroderm cells (and associated zooxanthellae) from semi-bleached rather than healthy sections (Salih et al. 1998, Harithsa et al. 2005, Ladriere et al. 2008). On the contrary, release of mucus-polysaccharide and mucus-lipid has been explained here to be consistent with beneficial (photoprotection) and detrimental (photo-damage) consequences arising from the predicted occurrence of CO_2 -limiting conditions within the intracellular zooxanthellae during periods of excess irradiance (sensu Wooldridge 2009). This new explanation need not diminish the significance of coral mucus secretions for other important homeostatic functions such as desiccation resistance, defence against pathogens, feeding and sediment cleaning. Furthermore, it does not diminish the possibility that other host-symbiont processes may be responsible for different forms of mucus production and release. Indeed, the highly variable composition and lack of universal structure of coral mucus argue against a single 'catch-all' process (reviewed by Brown & Bythell 2005).

The proposed role of mucus-polysaccharides in limiting photophysiological damage within the zooxanthellae population contributes to the growing awareness of the fundamental importance of the coral host in maintaining the stability and functioning (i.e. resilience) of the intact symbiosis (Baird et al. 2009, Wooldridge 2009, Wooldridge & Done 2009). In fact, the postulated existence of a host-to-symbiont carbon cycle appears to provide important context as to why specific components of host tissue homogenate (so-called 'host factors'; HFs) enhance photosynthate release and carbon fixation in freshly isolated zooxanthellae (FIZ) (Gates et al. 1995). In the *in vitro* setting, the HFs have been identified as FAAs, in particular taurine (Wang & Douglas 1997, Cook & Davy 2001). Of significance is the understanding that the catabolism of taurine leads to the 2-carbon product acetate

(Moran et al. 1994) and that FIZ always exhibit photoinhibition (Muller-Parker 1984, Stambler 1992). Comparative inference (Fig. 5) therefore permits the suggestion that FIZ are vulnerable to CO₂-limitation (and subsequent photoinhibition) when exposed to the unacclimatized *in vitro* experimental media and irradiance conditions. The inclusion of host tissue homogenate, rich in FAAs and lipid precursors, therefore provides FIZ with the opportunity to maintain lipid synthesis as an alternative sink for excess photosynthetically generated ATP and NADPH. This explanation diminishes support for the notion that HF's contain signalling molecules that cause photosynthetically derived carbon to be diverted away from zooxanthellae metabolism for release to the coral host (*sensu* Wang & Douglas 1997). Rather, it favours the idea that HF's are substrates that can be directly utilized by the zooxanthellae to produce an array of lipid compounds that are subsequently released to the host. Moreover, this new explanation diminishes support for the function of HF's as natural 'enhancers' of zooxanthellae physiological processes, but rather considers HF's alongside other host strategies (e.g. CCMs, MAAs and FPs) that seek to maintain the photosynthetic competency of the zooxanthellae during periods of high light flux, thereby ensuring the continued receipt of energy-rich photosynthates needed to maintain the stability of the intact symbiosis.

That heterotrophic catabolism helps underpin this homeostatic function highlights the potential for coral species that are well suited to external feeding and/or are capable of maintaining thick tissue reserves to display enhanced tolerance of 'bleaching' conditions that promote photophysiological damage of zooxanthellae. This is consistent with the fact that: (1) heterotrophic feeding helps to sustain photosynthetic quantum yields in symbiotic reef corals during thermal stress (Borell & Bischof 2008), and (2) mucus production predominates in the thick-tissued massive species (Richman et al. 1975) that display the greatest resistance to the bleaching syndrome (Marshall & Baird 2000, Loya et al. 2001). Indeed, the susceptibility of symbiotic corals to bleaching displays strong coherence with the extent of reduction/depletion of storage lipids during 'bleaching' conditions (Yamashiro et al. 2005).

Declines in coral mucus production rates across the duration of bleaching events (Glynn et al. 1985) are likely to reflect the depletion in somatic tissue reserves that accompanies prolonged bleaching events (Szmant & Gassman 1990, Yamashiro et al. 2005). Interestingly, an outlined thermal bleaching sequence for a population of massive *Porites* spp. identifies mass release of zooxanthellae only upon depletion of tissue reserves below a common lower-threshold (True 2005). A similar pre-bleaching se-

quence has also been noted for a branching *Acropora* sp. (Ainsworth et al. 2008). In this case, a significant reduction in the thickness of the outer coral tissue layer (epithelium) was observed several days before the onset of bleaching (= zooxanthellae expulsion) or reduction in dark-adapted photosynthetic yields (= PSII disruption). The authors identify excess mucus release and subsequent depletion of mucus reserves as the likely cause of this reduction in epithelial tissue thickness. Such evidence lends increasing support to the suggestion that the breakdown (disruption) of host homeostatic strategies may ultimately trigger the coral bleaching response (Wooldridge 2009, Wooldridge & Done 2009).

The important stabilising (combative) role performed by the coral host highlights the absolute necessity for future experiments to be conducted on the intact 'holobiont' (and not the individual partners) in order to gain a more complete understanding of the functioning and breakdown of the coral-algae endosymbiosis. For example, experiments on isolated zooxanthellae can be understood to have caused unnecessary confusion as to whether zooxanthellae release lipid products to the host *in symbio* (see e.g. Muscatine et al. 1994). Similarly, zooxanthellae in culture often produce no MAAs or a much reduced MAA complement (Banaszak & Trench 1995) implicating the *de novo* generation of the UVR-absorbing MAAs on host-to-zooxanthellae substrate transfer.

CONCLUDING COMMENTS

It is not the intent of this paper to evaluate or cast doubt on the importance of coral mucus secretion for previously ascribed homeostatic functions. Nor is the intent to establish a single 'catch-all' process for mucus production and release. Rather, attention has been directed at developing an integrated (conceptual) framework to help understand what enhanced coral mucus release during 'bleaching' conditions may reveal about the symbiotic condition(s) that trigger the breakdown of the coral-algae endosymbiosis. In this way, the enhanced release of both mucus-polysaccharide and mucus-lipid has been explained as consistent (i.e. not falsified) with the postulated role of CO₂-limitation within the 'dark' photosynthetic reactions of the algal endosymbionts as a key (universal) bleaching trigger (*sensu* Wooldridge 2009). Whilst it is acknowledged that further experimental testing is needed to strengthen this inference, if true, it supports the often ignored (potentially dominant) role of the coral host partner in maintaining the resilience of the symbiotic association in the face of environmental stress.

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