Prospects & Overviews

Is the coral-algae symbiosis really 'mutually beneficial' for the partners?

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The consideration of 'mutual benefits' and partner cooperation have long been the accepted standpoint from which to draw inference about the onset, maintenance and breakdown of the coral-algae endosymbiosis. In this paper, I review recent research into the climate-induced breakdown of this important symbiosis (namely 'coral bleaching') that challenges the validity of this long-standing belief. Indeed, I introduce a more parsimonious explanation, in which the coral host exerts a 'controlled parasitism' over its algal symbionts that is akin to an enforced domestication arrangement. Far from being pathogenic, a range of well-established cellular processes are reviewed that support the role of the coral host as an active 'farmer' of the energy-rich photoassimilates from its captive symbionts. Importantly, this new paradigm reposes the deleterious bleaching response in terms of an envelope of environmental conditions in which the exploitative and captive measures of the coral host are severely restricted. The ramification of this new paradigm for developing management strategies that may assist the evolution of bleaching resistance in corals is discussed.

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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') (Box 1) [1, 2]. Within this association, often mixed consortia of zooxanthellae types reside within the gastrodermal cells of the animal host and perform intensive photosynthesis (Fig. 1A). The vast majority (~95%) of this assimilated organic carbon ('photosynthate') is typically translocated to the coral, contributing substantially to its carbon and energy needs [3, 4]. For their part, the zooxanthellae receive protection from external predators whilst receiving access to host-derived substrates, principally carbon dioxide ($CO_{2(aq)}$) and ammonium (NH_4^+) [3, 4].

Despite its widespread conceptual appeal, in this paper I reconsider the mutualistic status of this 'producer-within-consumer' relationship, noting that symbioses are inclusive of a variety of interactions that occur along a continuum including mutualistic, commensal and parasitic associations[10]. The evolutionary process of natural selection cautions scientists to carefully consider apparent mutualistic symbioses. Selection shapes organisms to maximise individual fitness and conflict of interests are expected to arise whenever non-relatives interact. Such conflicts pose a challenge for the maintenance of mutualisms because each partner might benefit most from either exploiting or abandoning the other [11]. Attempts to reconcile evolutionary pathways leading to the onset and maintenance of mutualisms must therefore demonstrate that each organism can provide some benefit to its partner so that the success of one is bound to the success of the other; *i.e.* mutualism requires that both partners maintain benefits that exceed the costs [12, 13]. Thus far, a number of conflict avoidance factors have been identified as crucial for the continuous achievement of this mutualistic requirement. Following Herre *et al.* [13] these factors include: (i) vertical transmission, (ii) genetic uniformity of symbionts within the host and (iii) restricted options outside the relationship. However, as considered in this review, none of these features are universally employed by the coral-algae symbiosis.
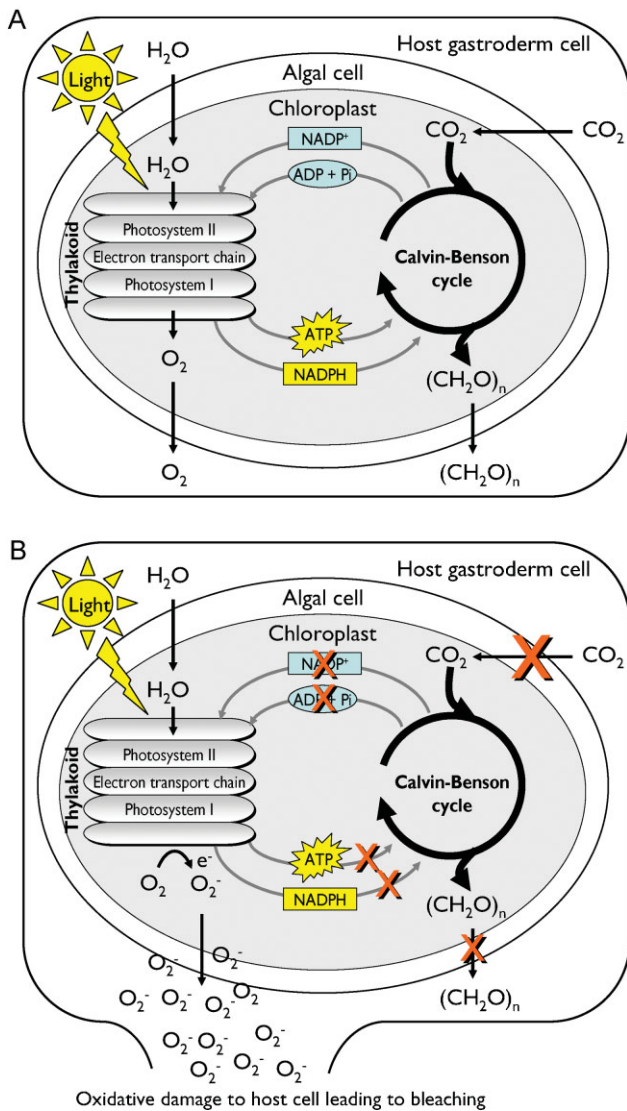
Review essays

Figure 1. A: Conceptual overview of the internal carbon cycling that is maintained by the coral-zooxanthellae symbiosis. 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 ($\sim$95%) of the assimilated photosynthates ($(CH_2O)_N$) are typically transferred to the coral host. **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 (according to Wooldridge [17]). 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.

The classical experimental test for mutualism is to evaluate the performance of organisms before and after its partner has been removed. For the coral-algae symbiosis, such experiments demonstrate that the symbiotic condition can deliver substantial growth and reproduction benefits to the coral host [3, 4], highlighting that the zooxanthellae are beneficial for the coral host in most situations. However, the benefit of the symbiotic condition for the zooxanthellae is more equivocal. For example, zooxanthellae growth rates when in symbiosis,

where doubling times are on the order of 70–100 days [14], are significantly slower than for the equivalent zooxanthellae in culture, where doubling times are approximately three days [15]. Such a result implies a fitness cost to the zooxanthellae whilst in symbiosis, which by definition is symptomatic of a parasitic relationship. The strength of this inference is, however, limited by the extent to which culture conditions share equivalence with the external environment experienced by zooxanthellae in their free-living state.

The breakdown of the coral-algae symbiosis in which the zooxanthellae are expelled *en masse* (namely coral bleaching) [16] provides an additional focal point to understand the nature of this symbiotic association. Recent experimental findings that detail the altered physiological states of the symbiont partners in the period leading up to (and including) climate-induced bleaching events thus provide a wealth of new information with which to test the parsimony of competing ideas. In a recent synthesis of this information, Wooldridge [17] identified the onset of CO_2 limitation within the 'dark reactions' of zooxanthellae photosynthesis as a potential unifying cellular mechanism for the classic bleaching sequence of zooxanthellae photoinhibition, oxidative damage, and host cell disruption (Fig. 1B).

In this way, biophysical factors that cause the demand for $CO_{2(aq)}$ to exceed supply within the coral's intracellular milieu are identified as bleaching risk factors (Fig. 2). In terms of the demand for $CO_{2(aq)}$, an enlarged endosymbiont population increases the likelihood of $CO_{2(aq)}$ becoming a limiting internal substrate during periods of peak photosynthesis [18, 19]. Several environmental factors favour increased zooxanthellae densities (particularly on a per host cell basis), including: (i) elevated nutrient levels (*e.g.* dissolved inorganic nitrogen, DIN) in the surrounding sea water [20], elevation of the CO_2 partial pressure (pCO_2) in the surrounding sea water [21], and diffusive (*i.e.* branching) coral colony morphologies [22]. Experimental manipulations confirm the higher expulsion rate of zooxanthellae during periods of high irradiance in branching corals [23] and in corals exposed to DIN and pCO_2 enrichment [24, 25].

However, since a coral's total photosynthetic demand for $CO_{2(aq)}$ is determined by the dynamic interplay between zooxanthellae population density and solar irradiance levels, a decline in either should return equilibrium and terminate the expulsion process. The problem arises in circumstances where an initial irradiance-driven reduction in zooxanthellae numbers also triggers disruption in the supply of $CO_{2(aq)}$ for the remnant zooxanthellae population. A range of host enzymes which function as active 'CO_2-concentrating mechanisms' (CCMs) underpin the bulk supply of $CO_{2(aq)}$ for the intracellular zooxanthellae (Box 2). A tight-cycling between the cellular energy needed to activate the CCMs and the receipt of photosynthates from the zooxanthellae [26, 27, 28, 29] dictates that the zooxanthellae indirectly play a role in generating the $CO_{2(aq)}$ that they themselves require for photosynthesis. 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 a proportion of the zooxanthellae vulnerable to CO_2 limitation (and expulsion), thereby further enhancing the reduction in photosynthate flux.

Box 1

Symbiodinium ('zooxanthellae')
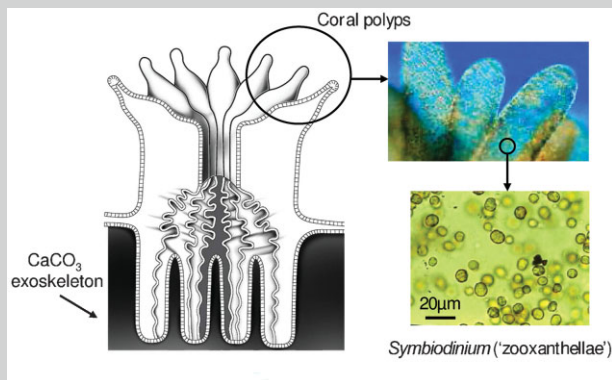
A reef coral is a symbiotic association between an animal (the host) and unicellular dinoflagellate algae (the symbionts). Within this association, the dinoflagellate algae of the genus *Symbiodinium* ('zooxanthellae') reside within the gastrodermal cells of the coral host. Originally it was believed 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 [5]). The genetically diverse zooxanthellae types differ in their phenotypic response (*e.g.* growth rate, photosynthetic yield) to external conditions, particularly light and temperature regimes [6, 7]. Modern genomic techniques demonstrate that many coral species can associate with multiple zooxanthellae types (often simultaneously). In this case, the symbiosis is typically dominated by one type, with other types present at low and previously undetectable 'background' levels [8]. The extent to which this flexibility is available to all symbiotic corals remains uncertain [5, 9].

Wooldridge [17] links the proximal driver of this destructive (self-enhancing) feedback to the specific growth rate ('mitotic index', MI) of the remnant zooxanthellae population following an initial irradiance-driven expulsion event, which is a synergistic function of temperature, nutrient availability and zooxanthellae type. When a large number of zooxathellae are expelled (per day) and then subsequently produced (per day), the increased respiratory cost of such turnover can lead to a negative autotrophic balance [30] where more carbon per day is directed into new cell production than is transferred to the coral host. This inverse relationship between photosynthate transfer and symbiont MI has been documented in corals, sea-anemones and jellyfish [31, 32, 33]. Indeed, the differential expulsion of zooxanthellae with high MI compared with those retained in the symbiosis [34, 35] supports the deleterious impact of high zooxanthellae MI on the localised stability of the symbiosis during bleaching conditions.

The key inference arising from the bleaching sequence outlined by Wooldridge [17] 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. In this paper, it is my intent to synthesise the available 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.

The coral host as an active 'farmer' of its captive photosynthetic symbionts

Numerous host-controlled processes are fundamental to the onset, maintenance and breakdown of the coral-algae endosymbiosis (Fig. 3). In this section, I review these processes to demonstrate how their integrated functioning is consistent with the proposed role of the host as an active 'farmer' of its photosynthetic symbionts.

Symbiont acquisition ('capture')

Uptake of symbionts from the ambient environment at every generation is by far the most common acquisition mode (>85%) in cnidarian species hosting zooxanthellae [36]. In this case, the host utilises chemosensory 'attractants' to lure free-living zooxanthellae within proximity to their coelenteral mouth, whereupon they are engulfed into the gastric cavity [37, 38]. The zooxanthellae are subsequently ingested into the endodermal cells lining the gastric cavity [37, 39]. The capture and uptake process is initially non-selective in terms of the different types of zooxanthellae [40, 41, 42]; however, a progressive winnowing process occurs over time (hours to years), so that only one to a few zooxanthellae types establish the long-term symbioses that are characteristically found in adults [9, 43]. Emerging evidence [44, 45] indicates that this winnowing process is largely driven by the symbiotic performance of the zooxanthellae, in particular the capacity to maintain photosynthate transfer across a hierarchy of constraints, including: (i) the abiotic and biotic conspecifics of the intracellular habitat, (ii) the microenvironment created by the skeletal morphology of the coral colony and (iii) the variable envelope of external environmental conditions. Indeed, experimental manipulations highlight that whilst photosynthetically inhibited zooxanthellae are initially taken up, they are quickly labelled by specific host-binding proteins which permit lysosomal fusion and subsequent degradation [46].

Symbiont 'domestication' and waste management

Once ingested, the zooxanthellae are surrounded by a host-derived 'symbiosome' membrane, which separates them from the cytoplasm of the host cell [47] and thus delineates their constrained (in hospite) environment. In its free-living state, zooxanthellae can exist as motile zoospore [48]. However,
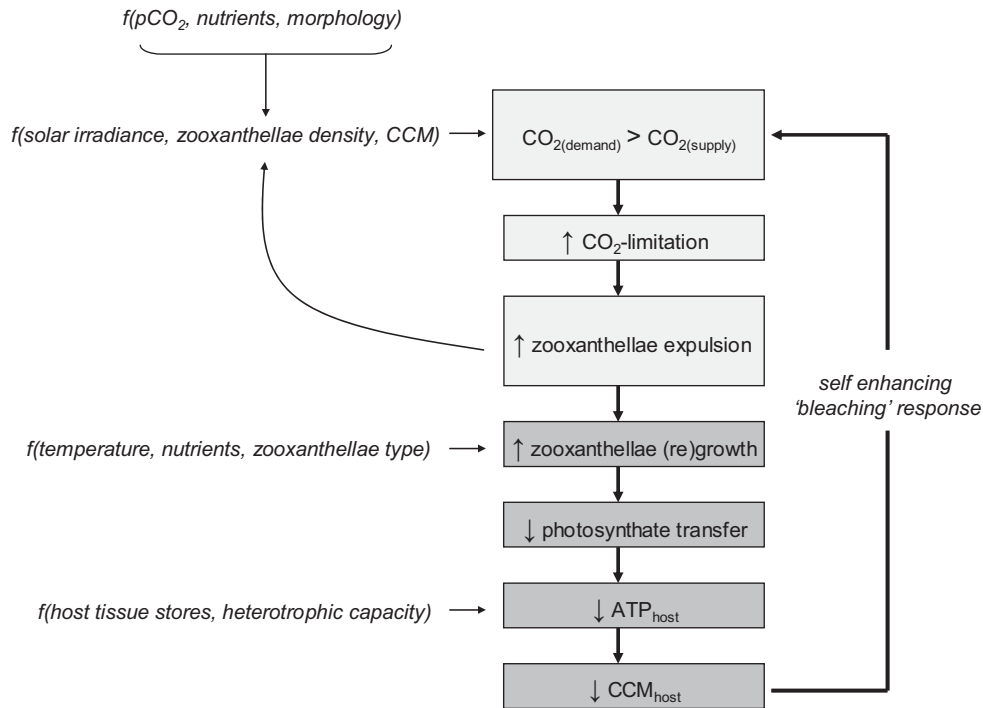
$f(pCO_2, nutrients, morphology)$

$f(solar\ irradiance, zooxanthellae\ density, CCM)$ → $CO_{2(demand)} > CO_{2(supply)}$

↑ CO_2-limitation

↑ zooxanthellae expulsion

self enhancing 'bleaching' response

$f(temperature, nutrients, zooxanthellae\ type)$ → ↑ zooxanthellae (re)growth

↓ photosynthate transfer

$f(host\ tissue\ stores, heterotrophic\ capacity)$ → ↓ ATP_{host}

↓ CCM_{host}

Figure 2. Schematic overview of the biophysical factors that interact to determine the demand- and supply-side dynamics for $CO_{2(aq)}$ substrate within the intracellular endosymbiont population. Factors that promote enlarged zooxanthellae densities increase $CO_{2(aq)}$ demand whilst factors that promote high zooxanthellae growth rates ultimately decrease $CO_{2(aq)}$ supply *via* ATP limitation of host 'CO$_2$-concentrating mechanisms' (CCMs). Factors that can forestall ATP limitation help to maintain the CCMs (according to Wooldridge and Done [105]). The notation f(factors) indicates a function of those factors.

once internalised, chemical signalling by the host arrests the zooxanthellae life cycle within a cell-dividing (vegetative) non-motile state [48, 49].

To reap the caloric benefits of housing photosynthetic zooxanthellae, the coral host must expose itself to sunlight, which includes not only photosynthetic available radiation (PAR, 400–700 nm) but also damaging ultraviolet radiation (UVR, 280–400 nm), conditions that are normally avoided by non-symbiotic epifauna [50]. To counter the threat of UVR-induced cellular damage, the coral host coordinates the accumulation of mycosporine-like amino acids (MAAs) within its tissues [51, 52, 53]. The MAAs function as biochemical sunscreens that absorb UVR and dissipate UV energy as heat without forming potentially toxic, reactive intermediates such as free radicals [52, 53].

The coral host also provides 'waste treatment' of the photosynthetic by-products (namely O$_2$) from the zooxanthellae. Before photosynthetic O$_2$ diffuses to the external sea water, it causes local hyperoxia (two- to three-fold above atmospheric normoxia) within the symbiosome and host tissues [54, 55]. Hyperoxia enhances the photodynamic generation of reactive oxygen species (ROS), among them free radicals, which, if unchecked, produce oxidative stress involving oxidation of membrane lipids, DNA or proteins, and thereafter cellular

ageing and death [55, 56]. The host's treatment of ROS is two-fold: firstly, the host maintains a range of ROS-scavenging systems, including enzymatic antioxidants such as superoxide dismutases, catalases and peroxidases, that detoxify ROS [54, 56]. Secondly, the host can initiate programmed cell death to selectively delete host cells containing dysfunctional (excessively ROS-generating) symbionts [57, 58].

Optimal 'harvest' strategies

Maximise symbiont photosynthesis
The intracellular location of zooxanthellae dramatically affects the supply of $CO_{2(aq)}$ needed for carbon fixation within the 'dark reactions' of photosynthesis. A limited availability of $CO_{2(aq)}$ can trigger the deleterious sequence whereby the conversion of PAR through the 'light reactions' of photosynthesis becomes stalled, so-called photoinhibition [59]. Photoinhibition reduces the efficiency of photosynthetic carbon fixation, and in extreme cases can initiate the bleaching response [7, 30]. To enhance the intracellular supply of $CO_{2(aq)}$ needed for optimal photosynthesis, the coral host maintains a range of active CCMs (Box 2). Importantly, the linkage of these CCMs to the receipt of photosynthates also represents a strong disincentive for zooxanthellae to shift towards parasitism (cheating). In essence, stability is maintained because 'defectors' (exploiters) become victims of their own success. If the zooxanthellae fail to invest in the host, they will generate local selection, *i.e.* CO_2 limitation → expulsion → replacement.

The CCMs are complemented by additional host-controlled processes that attenuate the peak flux of PAR entering the photosynthetic 'light reactions' of the zooxanthellae, thereby reducing excess (endpoint) demand for $CO_{2(aq)}$ within the photosynthetic 'dark reactions'. For example, fluorescent pigment proteins within host tissues help to lower the incidence of chronic photoinhibition by absorbing, scattering and

Box 2
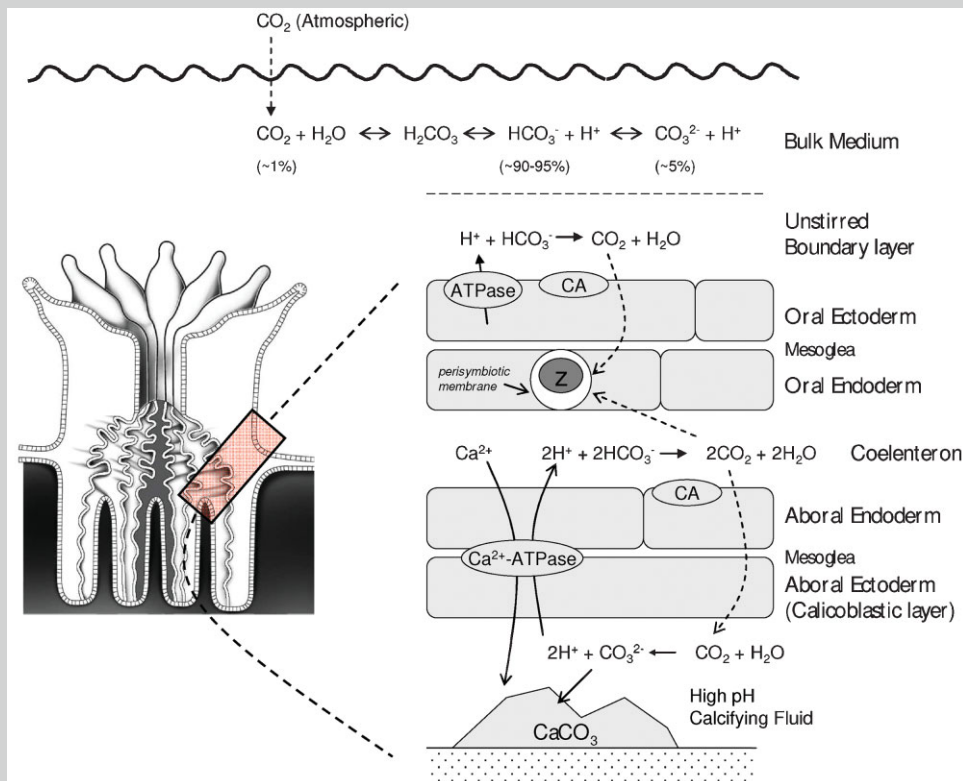
To enhance the intracellular supply of $CO_{2(aq)}$ for its zooxanthellae (Z), the coral host maintains a range of active CCMs. These CCMs supplement respiratory $CO_{2(aq)}$ by providing access to DIC available from the sea water, the most abundant form (>90%) of which is membrane-impermeable HCO_3^-. The efficient conversion of sea water HCO_3^- into readily diffusible $CO_{2(aq)}$ requires the expenditure of metabolic energy in the form of adenosine triphosphate (ATP). For example, at the ectodermal surface, hydration of HCO_3^- to $CO_{2(aq)}$ is achieved via an H^+-ATPase enzyme in combination with carbonic anhydrase (CA) [26, 27]. Similarly, by functioning to increase the availability of $CO_{2(aq)}$ within the coelenteron, the Ca^{2+}-ATPase enzyme that underpins host skeletal accretion also represents an important energy-driven CCM [28, 29]. The ATP needed to activate the CCMs is ultimately derived from the autotrophic carbon products of the zooxanthellae. For example, the quick release of energy-rich photosynthates (within 1 min of fixation) [3] ensures the rapid activation of the Ca^{2+}-ATPase enzyme [29]. This tight-cycling of autotrophic carbon dictates that the zooxanthellae effectively 'pay' for the delivery of $CO_{2(aq)}$ that they require to maintain optimal photosynthesis.

dissipating high-energy PAR by fluorescence [60]. Similarly, the typical daytime retraction of coral polyps in high-light environments functions as an efficient photoprotection mechanism for the contained zooxanthellae [61].

Maximise transfer of symbiont photosynthates
The coral host maintains intracellular (symbiotic) conditions that help to ensure its bulk receipt (>95%) of the fixed-carbon products. In the first instance, this includes processes which maintain the zooxanthellae in a growth-limited state; i.e. by restricting the intracellular availability of essential nutrients (especially NH_4^+) needed to undertake algal cell cytokinesis, the host can arrest zooxanthellae growth and compel the bulk transfer of fixed-carbon products [62, 63]. Whilst eutrophic conditions may limit the effectiveness of these processes, the host tissue activity of the NH_4^+- assimilating enzyme, glutamine synthetase (GS), is fundamental in ensuring the

nitrogen-limited growth state of the zooxanthellae in more optimal (oligotrophic) conditions [4]. Importantly, the efficiency of the GS enzyme is dependent on ATP. This dictates that the effectiveness of the host in maintaining the zooxanthellae growth-limited is modulated via its receipt of autotrophic carbon (energy), as evidenced by the significantly higher GS activity in symbiotic than in aposymbiotic animals [64], here again illustrating how the stability of the symbiosis benefits from the parasitic control of the host.

The diversion of photosynthates away from zooxanthellae metabolism towards release is further stimulated by putative 'host factor' (HF) signalling molecules [65, 66]. Recently, Wooldridge [67] proposed a cellular pathway linking the HF response to an integrated host-symbiont lipogenesis sequence, which also functions as a photoprotective mechanism during periods of excess irradiance. Importantly, the identified HF molecules originate from digestive metabolism that includes
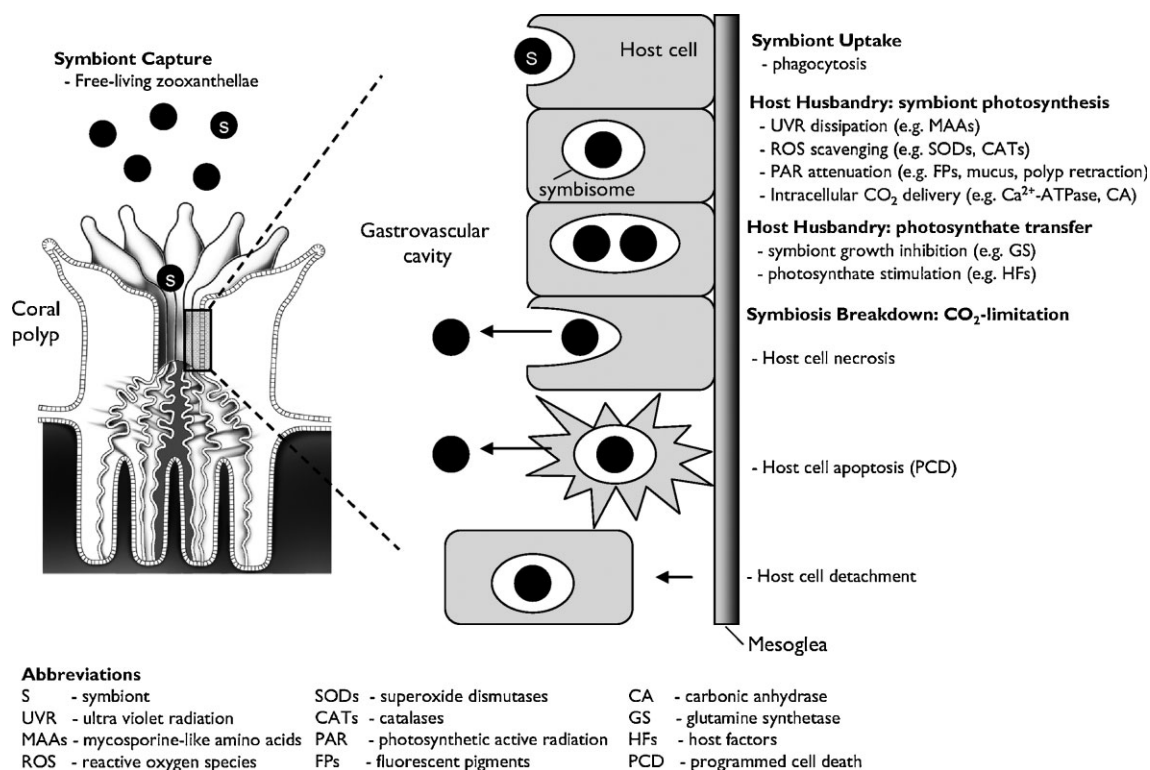
Figure 3. Host-controlled cellular processes that underpin the onset, maintenance and breakdown of the coral-algae endosymbiosis. Additional details surrounding the operation of these processes are provided within the main body of text.

heterotrophic feeding and/or catabolism of host tissue reserves. Though requiring further experimental verification, this host 'husbandry' process may assist in explaining why heterotrophic feeding helps to sustain the photosynthetic quantum yield of zooxanthellae even during periods that are sub-optimal for 'normal' carbon assimilation [68].

Maximise symbiont diversity

Many coral species maintain simultaneous symbiosis with more that one zooxanthellae type (Box1). Phenotypic trait variations within the cosmopolitan consortia provide the opportunity for specific zooxanthellae types to be superior/ inferior symbionts when exposed to different environmental conditions. In this way, dynamic 'shuffling' in the relative dominance of different zooxanthellae types is understood to maximise the receipt of photosynthates by the coral host across the entire dynamic (seasonal) range of environmental conditions [69].

Wooldridge [17] outlines a passive host mechanism by which the relative dominance of the different zooxanthellae types dynamically reshuffle based on their comparative temperature-dependent growth characteristics, with faster growing zooxanthellae being superior competitors for available host habitat during cooler (low irradiance) conditions, and slower growing zooxanthellae favoured in warm (high irradiance) conditions. This mechanism is underpinned by the

highlighted ability of the coral host to differentially expel zooxanthellae that exceed 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. In essence, the coral host utilises the differential growth rates and competition that exists between zooxanthellae types [44, 70] to maintain a dynamic symbiont population that is optimally matched to the prevailing conditions, particularly in terms of photosynthate delivery. This ability to detect and expel exploiters may help to explain why the coral symbiosis does not confirm virulence theory in its prediction that hosting of multiple symbiont genotypes should promote the evolution of symbiont exploitation (parasitism) of the host [71].

Symbiosis breakdown (= loss of parasitic control)

An easily identified Achilles' heel of the zooxanthellae domestication arrangement outlined here is the necessary requirement for tight-cycling of autotrophic energy. It follows that any external environmental perturbation that disrupts the transfer of photosynthates to the coral host can quickly erode its parasitic control and lead to the breakdown of the symbiosis. In support of this interpretation, disruption in autotrophic capacity is known to precede the thermal expulsion of zooxanthellae [72, 73], which is accompanied by an increase in MI of the remnant zooxanthellae in hospite[23, 35]. Wooldridge [17] explains this coral bleaching sequence in terms of an energy-dependent loss of control by the host of the intracellular conditions experienced by the zooxanthellae (namely the availability of $CO_{2(aq)}$ and NH_4^+). A self-enhancing downward spiral triggered by PAR-induced CO_2 limitation

($=$ zooxanthellae expulsion) and progressively unconstrained ($=$ NH_4^+-replete) division of the remnant zooxanthellae ensures that a greater proportion of autotrophic carbon is directed into new algal cell production than is transferred to the coral host, further compromising the host's energy requirements needed to maintain parasitic control of the symbiosis.

Only upon the reduction in PAR and/or a lowering in zooxanthellae division rates (as mediated by lower temperatures) can the coral host re-establish a beneficial association. Where available, zooxanthellae reshuffling in favour of slow-growing zooxathellae types (*e.g.* clade D *Symbiodinium* spp.; R. Berkelmans, unpublished data) can enhance resistance to this deleterious breakdown sequence [74]. However, once mass expulsion of zooxanthellae has occurred, it is ultimately the potential of the coral to derive alternate caloric input from heterotrophic catabolism that defines its survival prospects in the interim period (several weeks) until the symbiosis can be re-established [75]. This outlined bleaching sequence is commensurate with the paradoxical observation that the majority of expelled zooxanthellae remain photosynthetically competent [76], since it is the failure to transfer photosynthates rather than compromised photosynthetic capacity *per se* that is predicted to be the ultimate driver of the self-enhancing expulsion dynamic.

An alternative triggering agent for bleaching, namely prolonged exposure to darkness, provides additional evidence that the breakdown of cnidarian symbioses represents a release of the algal partner from its host control. For example, a cnidarian host can loose >50% of its zooxanthellae when exposed to darkness for more 10 days [77]. However, as predicted by the energy-dependent release of the zooxanthellae from its demographic control by the host, the darkness treatment also gives rise to a transient (2–4 days) increase (two- to three-fold) in the MI of the zooxanthellae, before its eventual decline [77]. It is thus consistent that coral colonies found at low-irradiance sites, whether due to depth or turbidity, are often differentially populated by slow-growing Clade D zooxanthellae [78, 79], reinforcing the earlier prediction that reef conditions that are sub-optimal for photosynthate transfer should favour the host's establishment of symbionts with slow intrinsic growth dynamics.

Controlled parasitism: A general host strategy for the 'producer-within-consumer' relationship?

Based on the contextual evidence outlined here, it is apparent that the conventional labelling of the coral-algae symbiosis as 'mutually beneficial' is tantamount to believing that domestic dairy cattle and humans have a comparable relationship because we provide them with food and shelter and regulate their population before we harvest (exploit) their milk production. Given the numerous examples in nature where inherent parasitism is detrimental (even lethal) to the enacted partner, it is not surprising that it is difficult for scientists to reconcile the widespread evolutionary success of the coral-algae symbiosis with a parasitic underpinning.

However, the negative connotation of parasitic relationships most readily fits with the exploitation of hosts by unwelcome symbionts. The notion of hosts exploiting their symbionts is less evident, yet precedent examples have been suggested wherein a controlled manipulation by the host can facilitate a stable and persistent relationship. For example, the lichen symbiosis has been explained in terms of a controlled parasitism by the fungal (host) on its photobionts (green alga/cyanobacterium) [80]. As detailed here for the coral-algae symbiosis, the growth and reproduction of the photobionts in lichen symbiosis are restrained and controlled by the fungus host in order to optimise the 'harvest' of photoassimilates [81]. A similar controlled parasitism has been proposed for the association between certain marine invertebrate species (*e.g.* clams, mussels and tube worms) and chemosynthetic bacteria, which flourish upon hydrothermal vents in the unlit recesses of the deep ocean [82].

The reluctance to assign the lowered reproductive capacity of in hospite zooxanthellae to a parasitic host has largely arisen from the belief that symbiosis-forming zooxanthellae are unable to survive and flourish in free-living forms within tropical reef habitats. However, this belief originates from a significant knowledge gap with regard to the presence and diversity of free-living zooxanthellae within the water column surrounding reef habitats. Only recently studies have started to document the existence of a free-living 'pool' of *Symbiodinium* genotypes, with the emerging evidence indicating that a diverse population of symbiosis-forming zooxanthellae types flourish in the sediment and sea water adjacent to Ref. 8384 [85], including the potential displayed by certain types to alternate between a free-living and an endosymbiotic lifestyle [86]. This indicates that the zooxanthellae are unlikely to be solely dependent upon the intracellular host habitat in order to ensure their ecological persistence. In the same way, alga in the lichen symbiosis can thrive and grow faster when free-living than in symbiosis [80], whilst sulphide-oxidising bacteria survive and flourish in a free-living state, whereas their invertebrate hosts are completely unable to do so [82].

The existence of an environmental pool of free-living *Symbiodinium* provides the coral host with the opportunity to interact and potentially select from these populations, thereby perpetuating their endosymbioses. Specific individuals within these free-living assemblages may currently be excluded from engaging in endosymbiotic interactions with coral hosts, depending on their competitive abilities to proliferate in the host and maintain optimal photosynthate transfer. However, if environmental conditions select against the current endosymbiotic complement, alternative individuals from the free-living state may suit the newly available endosymbiotic niche. Periodic 'switching' of the endosymbiont population with opportunistic zooxanthellae types helps to explain the lack of congruence between *Symbiodinium* and coral host phylogenies [5, 87]. Periodic switching of symbionts from an external free-living population also explains the lack of host-symbiont coevolution within lichen, protist and chemosynthetic symbioses [88, 89, 90].

Despite lower reproductive rates in hospite, it is often argued that *Symbiodinium* may have benefited from a wider distribution and overall abundance through their association with corals and other marine invertebrates. Indeed, whilst

there is no correlation between host and symbiont phylogenies at the scale of clades, higher levels of coevolution are evident at the lower taxonomic ranks [5]. This identifies allopatric differentiation within the host habitat as a potentially important driver of *Symbiodinium* diversification during the Cenozoic [91]. In this case, intense selection pressure within the host cytoplasm, aided by symbiont competition and variable external environmental conditions, is predicted to generate small founder populations susceptible to genetic drift and/or 'genetic revolutions'. In particular, because the host is capable of influencing the growth rate of zooxanthellae in hospite, natural selection may be driven to favour those traits that enhance the existing host regulation of demographic parameters of the symbiont. This notion of evolved traits that are suboptimal for independent survival in the free-living state has been used to argue against the ultimate mutual benefit of particular evolved symbiosis, including the coral-algae symbiosis [92, 93]. The basis of this conclusion bears direct comparison to the question of whether farmed animals ultimately benefit from their domestication, as witnessed by the fact that over one third of domestic animal breeds are currently at risk of extinction [94].

Modern sequencing and genomic techniques do provide an experimental avenue to test the host-controlled parasitism hypothesis. For example, it is consistent that no studies to date have identified any novel (symbiosis-specific) housekeeping genes for zooxanthellae (reviewed by Yellowlees *et al.* [4]). Moreover, in line with the host's control of the symbiosis, basic local alignment search tool (BLAST)-based approaches indicate extremely small contributions (1–6%) of the symbiont's genome to unique gene sequences in the mixed host-symbiont transcriptome [95]. Such evidence exists in opposition to the integrated host-symbiont transcriptome, which is expected to underpin the high levels of cooperation and specificity implicitly within mutualistic relationships. It is interesting to speculate that if the host is actively manipulating a controlled parasitism (with low symbiont specificity, other than selection based on photosynthate receipt) then it may not need to alter its own existing protein pathways significantly to engage the symbiosis. Such a suggestion finds support from the small number of differentially expressed host genes during the establishment of the coral-algae symbiosis [96], and lessens the reliance on speculation that this response is best explained in terms of the symbiont's ability to enter the host in a stealth manner.

Again, this contrasts the expected pattern for highly evolved mutualisms. For example, in accordance with the high levels of coevolution and host-symbiont specificity evident in the symbiosis between squid and luminous bacteria [97], it has been noted that many hundreds of genes are differentially expressed upon its initiation [98]. Based on the host-controlled parasitism standpoint, the most likely place to look for differentially expressed (or indeed novel) host genes will be in the outlined host's 'husbandry' functions associated with: (i) enhancing intracellular CO_2 supply, including its link to $CaCO_3$ deposition, (ii) moderating light-driven intracellular CO_2 demand, (iii) neutralising ROS, including programmed host cell death and (iv) maintaining the endosymbionts in a growth-limited state. Future genomic studies are needed to confirm the robustness of these predictions, though early evidence is consistent with the proposed bleaching sequence linking reduced calcification, increased oxidative stress and host cell death [99].

Implications for study and potential protection of corals undergoing bleaching

Acceptance of the host-controlled parasitism hypothesis provides a new standpoint from which to test the mechanistic details underpinning the potential evolution of bleaching resistance in response to future climate change. In particular, it focuses attention on the adaptive capacity of the host to maintain control of the reproductive traits (namely growth rates and density) of its endosymbionts as ocean temperatures and pCO_2 levels rise. Since the specific growth rate of many zooxanthellae types increases rapidly with rising temperatures (*e.g.* key representatives from clade C) [6, 23], this adaptive potential includes the capacity demonstrated by some corals to 'switch' or 'shuffle' their endosymbiont population with alternate zooxanthellae types that have lower kinetic growth rates (*e.g.* specific representatives from clade D; R. Berkelmans, unpublished data). For example, shuffling from clade C to clade D symbionts facilitates a 1–1.5 °C increase in the thermal bleaching threshold of *Acropora millepora* [74].

The complementary capacity of the host to enhance thermal bleaching resistance by constraining absolute densities of zooxanthellae (independent of the zooxanthellae type) is demonstrated by the known acclimatisation response of corals in which pre-exposure to environmental conditions that induce a lowering of the endosymbiont population helps to reduce the future susceptibility to bleaching. For example: (i) Coles and Jokiel [100] highlight that pre-treatments which left *Montipora verrucosa* semi-bleached assisted survival at higher temperatures; (ii) Brown *et al.* [101] demonstrate that exposure to a high solar radiation event (that lowered symbiont densities by ~15–20%) prior to maximal seasonal sea water temperatures helped to limit thermal bleaching in *Goniastrea aspera*; (iii) Ulstrup *et al.* [102] demonstrate that regional-scale differences in densities of zooxanthellae directly relate to the bleaching susceptibility in *Pocillopora damicornis*, with the corals that hosted larger zooxanthellae densities in the field showing the earliest and severest thermal stress in the laboratory and (iv) Berkelmans and Willis [103] found that during winter (when symbiont densities are typically higher by ~20–50%) [104], the bleaching threshold for *P. damicornis* was 1 °C lower than the summer threshold. In each of these examples, the zooxanthellae type was presumed to be uniform across treatments, highlighting that within reasonable functional limits, lower densities of zooxanthellae may confer greater bleaching resistance on many modern symbiotic corals. Moreover, it alludes to the loss of optimal host control of endosymbiont densities given modern environmental conditions.

Indeed, the emerging envelope of environmental conditions – characterised by elevated sea surface temperatures, rising pCO_2 and increased levels of inorganic nutrients – are clearly antagonistic to the outlined host processes that contribute demographic control to the endosymbiont population. For example, corals that are exposed to external nutrient

enrichment are characterised by enlarged, fast-growing zoox-anthellae populations [18, 20], and it is thus consistent that nutrient-enriched reefs are more susceptible to thermal disruption, with bleaching thresholds ~1–2 °C lower than for reefs with reduced levels of enrichment [105, 106]. Similarly, unchecked proliferation of photobiont populations and concomitant disruption of the symbiosis is a well-estab-lished response to excess nutrient fertilisation of lichens [107] and freshwater protozoa [108].

More research is needed to understand the entire suite of regulation mechanisms available to the coral host and how the emerging envelope of environmental conditions may conspire against (or potentially assist) their functional efficiency. The combination of nutrient sufficiency, elevated pCO_2 and increasing temperature is likely to be detrimental to the out-lined CO_2 limitation regulation strategy (Fig. 2), since an ever-increasing proportion of the symbiont population is released to function autonomously on environmental (diffusive) $CO_{2(aq)}$ and thereby reside outside of the strict host sanctioning that is implicit with the photosynthate feedback function of the CCMs.

It is noteworthy that the juxtaposition of the clocked phylogenetic tree for *Symbiodinium* with the long-term pat-terns in Cenozoic global climate reveals that the major diver-sifications in genotypes occurred during periods of global cooling and falling pCO_2 levels (Fig. 4). In this case, the progressive lowering of the constraint imposed by the 'poten-tial' thermal (kinetic) growth rate may be understood to have provided additional degrees of freedom for the selective enve-lope 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 sym-biosis necessitates that one of the other growth co-factors provides a limiting 'bottleneck' to the increasing thermal growth potential. On this note, it is consistent that present global locations which display the highest levels of bleaching resistance are united by extreme oligotrophic conditions in the warmer summer months (*e.g.* Red Sea) [109] and/or the pres-ence of zooxanthellae types that exhibit slow intrinsic growth dynamics (*e.g.* clade D) [74].

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. Moreover, it provides crucial insights into how 'local' water quality improvement strategies in combination with 'global' CO_2 reduction strategies may help to maintain the existing para-sitic control mechanisms and/or assist the adaptive capacity available to the coral host [105, 106].

Conclusions and prospects

It has long been realised that the coal-algae symbiosis is a finely tuned association, based on the 'slack' between photo-synthetic carbon assimilation and its retention for growth by the symbionts. Yet, the associated question of why the algal
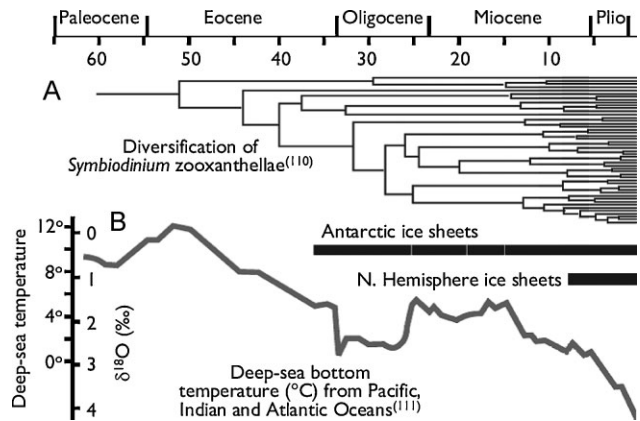

Figure 4. A: Chronogram of divergence timing of symbiotic dino-flagellate *Symbiodinium* established by molecular phylogeny. [110] *Symbiodinium* originated in the early Eocene, and most extant lin-eages diversified after the mid-Miocene, coinciding with the last cooling that followed the mid-Miocene climate optimum. **B**: Global deep sea oxygen record [111] as a proxy of deep sea temperature changes during the Cenozoic (adapted from Pomar and Hallock [112]).

partner would incur reproduction costs in order to benefit the coral host has remained perplexing. In this review, a much greater importance has been considered for the role of the coral host in the control of the symbiotic association. Far from being benignly mutualistic, it concluded here that the evol-utionary functioning of the coral host is best described in terms of a controlled parasitism in which the autonomous functioning of the symbionts is constrained and manipulated; a conclusion that appears broadly consistent for a range of alternative symbioses based on the producer-within-consumer relationship. Future testing of this new paradigm offers the hope of developing new insights into tackling climate-induced coral bleaching.

References

1. **Veron JEN.** 1995. *Corals in Space and Time: The Biogeography and Evolution of the Scleractinians*. Ithaca, New York: Cornell University Press.
2. **Stanley GD.** 2006. Photosymbiosis and the evolution of modern coral reefs. *Science* **312**: 857–8.
3. **Trench RK.** 1993. Microalgal-invertebrate symbioses: a review. *Endocytobiosis Cell Res* **9**: 135–75.
4. **Yellowlees D**, **Rees TA**, **Leggat W**. 2008. Metabolic interactions between algal symbionts and invertebrate hosts. *Plant Cell Environ* **31**: 679–94.
5. **Baker AC.** 2003. Flexibility and specificity in coral-algal symbiosis: diversity, ecology, and biogeography of *Symbiodinium*. *Annu Rev Ecol Evol Syst* **34**: 661–89.
6. **Kinzie RA**, **Takayama M**, **Santos SR**, *et al*. 2001. The adaptive bleach-ing hypothesis: experimental tests of critical assumptions. *Biol Bull* **200**: 51–8.

Review essays

7. **Rowan R.** 2004. Coral bleaching: thermal adaptation in reef coral symbionts. *Nature* **430**: 742.

8. **Mieog JC**, **van Oppen MJH**, **Cantin NE**, *et al*. 2007. Real-time PCR reveals a high incidence of *Symbiodinium* clade D at low levels in four scleractinian corals across the Great Barrier Reef: implications for symbiont shuffling. *Coral Reefs* **26**: 449–57.

9. **Goulet D.** 2006. Most corals may not change their symbionts. *Mar Ecol Prog Ser* **321**: 1–7.

10. **Leung TL**, **Poulin R.** 2008. Parasitism, commensalism and mutualism: exploring the many shades of symbioses. *Vie et Milieu – Life Environ* **58**: 107–15.

11. **Sachs JL**, **Simms EL.** 2006. Pathways to mutualism breakdown. *Trends Ecol Evol* **21**: 587–92.

12. **Axelrod R**, **Hamilton WD.** 1981. The evolution of cooperation. *Science* **211**: 1390–6.

13. **Herre EA**, **Knowlton N**, **Mueller UG**, *et al*. 1999. The evolution of mutualisms: exploring paths between conflict and cooperation. *Trends Ecol Evol* **14**: 49–53.

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

15. **Fitt WK**, **Trench RK.** 1983. The relation of diel patterns of cell division to diel patterns of motility in the symbiotic dinoflagellate *Symbiodinium microadriaticum* Freudenthal in culture. *New Phytol* **94**: 421–32.

16. **Brown BE.** 1997. Coral bleaching: causes and consequences. *Coral Reefs* **16**: 129–38.

17. **Wooldridge SA.** 2009. A new conceptual model for the warm-water breakdown of the coral-algae endosymbiosis. *Mar Fresh Res* **60**: 483–96.

18. **Dubinsky Z**, **Stambler N**, **Ben-Zion M**, *et al*. 1990. The effect of external resources on the optical properties and photosynthetic efficiency of *Stylophora pistillata*. *Proc R Soc Lond B* **239**: 231–46.

19. **Davy SK**, **Cook CB.** 2001. The relationship between nutritional status and carbon flux in the zooxanthellate sea anemone *Aiptasia pallida*. *Mar Biol* **139**: 999–1005.

20. **Muscatine L**, **Ferrier-Pages C**, **Blackburn A**, *et al*. 1998. Cell-specific density of symbiotic dinoflagellates in tropical anthozoans. *Coral Reefs* **17**: 329–37.

21. **Reynaud S**, **Leclercq N**, **Romaine-Lioud S**, *et al*. 2003. Interacting effects of CO_2 partial pressure and temperature on photosynthesis and calcification in a scleractinian coral. *Glob Chang Biol* **9**: 1660–8.

22. **Helmuth BST**, **Timmerman BEH**, **Sebens KP.** 1997. Interplay of host morphology and symbiont microhabitat in coral aggregations. *Mar Biol* **130**: 1–10.

23. **Strychar KB**, **Coates M**, **Sammarco PW.** 2004. Loss of *Symbiodinium* from bleached Australian scleractinian corals (*Acropora hyacinthus*, *Favites complanata* and *Porites solida*). *Mar Fresh Res* **55**: 135–44.

24. **Stimson J**, **Kinzie RA.** 1991. The temporal pattern and rate of release of zooxanthellae from the reef coral *Pocillopora damicornis* (Linnaeus) under nitrogen-enrichment and control conditions. *J Exper Mar Biol Ecol* **153**: 63–74.

25. **Anthony KRN**, **Kline DI**, **Diaz-Pulido G**, *et al*. 2008. Ocean acidification causes bleaching and productivity loss in coral reef builders. *Proc Nat Acad Sci (USA)* **105**: 17442–6.

26. **Furla P**, **Allemand D**, **Orsenigo MN.** 2000. Involvement of H^+-ATPase and carbonic anhydrase in inorganic carbon uptake for endosymbiont photosynthesis. *Am J Physiol Regul Integr Comp Physiol* **278**: 870–81.

27. **Al-Horani FA**, **Al-Moghrabi SM**, **De Beer D.** 2003. Microsensor study of photosynthesis and calcification in the scleractinian coral, *Galaxea fascicularis*: active internal carbon cycle. *J Exp Mar Biol Ecol* **288**: 1–15.

28. **McConnaughey TA**, **Whelan JF.** 1997. Calcification generates protons for nutrient and bicarbonate uptake. *Earth Sci Rev* **42**: 95–117.

29. **Al-Horani FA**, **Al-Moghrabi SM**, **De Beer D.** 2003. The mechanism of calcification and its relation to photosynthesis and respiration in the scleractinian coral, *Galaxea fascicularis*. *Mar Biol* **142**: 419–26.

30. **Hoogenboom MO**, **Anthony KRN**, **Connolly SR.** 2006. Energetic cost of photoinhibition in corals. *Mar Ecol Prog Ser* **313**: 1–12.

31. **Sachs JL**, **Wilcox TP.** 2006. A shift to parasitism in the jellyfish symbiont *Symbiodinium microadriaticum*. *Proc R Soc Lond B* **273**: 425–9.

32. **Verde AE**, **McCloskey LR.** 1996. Photosynthesis and respiration of two species of algae symbionts in the Anemone *Anthopleura elegantissima* (Brandt) (Cnidaria; Anthozoa). *J Exp Mar Biol Ecol* **195**: 187–202.

33. **McGuire MP**, **Szmant AM.** 1997. Time course of physiological responses to NH_4 enrichment by a coral-zooxanthellae symbiosis. In Lessios HA, Macintryre G, ed; *Proceedings of the 8th Coral Reef Symposium*. Panama: Smithsonian Tropical Research Institute. p. 909–14.

34. **Baghdasarian G**, **Muscatine L.** 2000. Preferential expulsion of dividing algal cells as a mechanism for regulating algal-cnidarian symbiosis. *Biol Bull* **199**: 278–86.

35. **Bhagooli R**, **Hidaka M.** 2002. Physiological responses of the coral *Galaxea fascicularis* and its algal symbiont to elevated temperatures. *Galaxea* **4**: 33–42.

36. **Richmond RH.** 1997. Reproduction and recruitment in corals: critical link in the persistence of reefs. In: Birkeland C, ed; *Life and Death of Coral Reefs*. New York: Chapman & Hall; p. 175–97.

37. **Fitt WK.** 1984. The role of chemosensory behaviour of *Symbiodinium microadriaticum*, intermediate hosts, and host behaviour in the infection of coelenterates and molluscs with zooxanthellae. *Mar Biol* **81**: 9–17.

38. **Pasternak Z**, **Blasius B**, **Abelson A**, *et al*. 2006. Host-finding behaviour and navigation capabilities of symbiotic zooxanthellae. *Coral Reefs* **25**: 201–7.

39. **Fitt WK**, **Trench RK.** 1983. Endocytosis of the symbiotic dinoflagellate *Symbiodinium microadriaticum* Freudenthal by endodermal cells of the scyphistomae *Cassiopeia xamachana* and resistance of the algae to host digestion. *J Cell Sci* **64**: 195–212.

40. **Coffroth MA**, **Santos SR**, **Goulet TL.** 2001. Early ontogenetic expression of specificity in a cnidarian-algal symbiosis. *Mar Ecol Prog Ser* **222**: 85–96.

41. **Little AF**, **van Oppen MJH**, **Willis BL.** 2004. Flexibility in algal endosymbiosis shapes growth in reef corals. *Science* **304**: 1492–4.

42. **Gómez-Cabrera M**, **Ortiz JC**, **Loh WKW**, *et al*. 2008. Acquisition of symbiotic dinoflagellates (*Symbiodinium*) by juveniles of the coral *Acropora longicyathus*. *Coral Reefs* **27**: 219–26.

43. **Dunn SR**, **Weis VM.** 2009. Apoptosis as a post-phagocytic winnowing mechanism in a coral-dinoflagellate mutualism. *Environ Microbiol* **11**: 268–76.

44. **Fitt WK.** 1985. Effect of different strains of zooxanthella *Symbiodinium microadriaticum* on growth and survival of their coelenterate and molluscan hosts. *Proc 5th Int Coral Reef Symp* **6**: 131–6.

45. **Cantin NE**, **van Oppen MJH**, **Willis BL**, *et al*. 2009. Juvenile corals can acquire more carbon from high-performing algal symbionts. *Coral Reefs* **28**: 405–14.

46. **Chen M**, **Hong M**, **Huang Y**, *et al*. 2005. ApRab11, a cnidarian homologue of the recycling regulatory protein Rab11, is involved in the establishment and maintenance of the *Aiptasia-Symbiodinium* endosymbiosis. *Biochem Biophys Res Commun* **338**: 1607–16.

47. **Wakefield TS**, **Kempf SC.** 2001. Development of host- and symbiont-specific monoclonal antibodies and confirmation of the origin of the symbiosome membrane in a cnidarian-dinoflagellate symbiosis. *Biol Bull* **200**: 127–43.

48. **Stat M**, **Carter D**, **Hoegh-Guldberg O.** 2006. The evolutionary history of Symbiodinium and scleractinian hosts – Symbiosis, diversity and the effect of climate change. *Perspect Plant Ecol Evol Syst* **8**: 23–43.

49. **Koike K**, **Jimbo M**, **Sakai R**, *et al*. 2004. Octocoral chemical signalling selects and controls dinoflagellate symbonts. *Biol Bull* **207**: 80–6.

50. **Jokiel PL.** 1980. Solar ultraviolet radiation and coral reef epifauna. *Science* **207**: 1069–71.

51. **Baird AH**, **Bhagooli R**, **Ralph PJ**, *et al*. 2008. Coral bleaching: the role of the host. *Tends Ecol Evol* **24**: 16–20.

52. **Shick JM**, **Dunlap WC.** 2002. Mycosporine-like amino acids and related gadusols: Biosynthesis, accumulation, and UV-photoprotective functions in aquatic organisms. *Annu Rev Physiol* **64**: 223–62.

53. **Furla P**, **Allemand D**, **Shick JM**, *et al*. 2005. The symbiotic anthozoan: a physiological chimera between alga and animal. *Integr Comp Biol* **45**: 595–604.

54. **Dykens JA**, **Shick JM.** 1982. Oxygen production by endosymbiotic algae controls superoxide dismutase activity in their animal host. *Nature* **297**: 579–80.

55. **Kühl M**, **Cohen Y**, **Dalsgaard T**, *et al*. 1995. Microenvironment and photosynthesis of zooxanthellae in sclearctinian corals studies with microsensors for O_2, pH and light. *Mar Ecol Prog Ser* **117**: 159–72.

56. **Lesser MP.** 2006. Oxidative stress in marine environments: biochemistry and physiological ecology. *Annu Rev Physiol* **68**: 253–78.

57. **Dunn SR**, **Bythell JC**, **Le Tissier MDA**, *et al*. 2002. Programmed cell death and cell necrosis activity during hyperthermic stress-induced bleaching of the symbiotic sea anemone *Aiptasia* sp. *J Exp Mar Biol Ecol* **272**: 29–53.

58. **Perez S**, **Weis VM.** 2006. Nitric oxide and cnidarian bleaching: an eviction notice mediates breakdown of a symbiosis. *J Exp Biol* **209**: 2804–10.

59. **Takahashi S**, **Murata N.** 2006. Glycerate-3-phosphate, produced by CO_2 fixation in the Calvin cycle, is critical for the synthesis of the D1 protein of photosystem II. *Biochim Biophys Acta* **1757**: 198–205.

60. **Salih A**, **Larkum A**, **Cox G**, *et al*. 2000. Fluorescent pigments in corals are photoprotective. *Nature* **408**: 850–3.

61. **Brown BE**, **Downs CA**, **Dunne RP**, *et al*. 2002. Preliminary evidence for tissue retraction as a factor in photoprotection of corals incapable of xanthophyll cycling. *J Exp Mar Biol Ecol* **277**: 129–44.

62. **Smith GJ**, **Muscatine L.** 1999. Cell cycle of symbiotic dinoflagellates: variation in G_1 phase-duration with anemone nutritional status and macronutrient supply in the *Aptasia pulchella-Symbiodinium pulchrorum* symbiosis. *Mar Biol* **135**: 405–18.

63. **Dubinsky Z**, **Berman-Frank I.** 2001. Uncoupling primary production from population growth in photosynthesising organisms in aquatic ecosystems. *Aquat Sci* **63**: 4–17.

64. **Wang JT**, **Douglas AE.** 1998. Nitrogen recycling or nitrogen conservation in an algae-invertebrate symbiosis? *J Exp Biol* **201**: 2445–53.

65. **Gates RD**, **Hoegh-Guldberg O**, **McFall-Ngai M**, *et al*. 1995. Free amino acids exhibit anthozoan 'host factor' activity: They induce the release of photosynthate from symbiotic dinoflagellates *in vitro*. *Proc Nat Acad Sci (USA)* **92**: 7430–4.

66. **Wang JT**, **Douglas AE.** 1997. Nutrients, signals and photosynthate release by symbiotic algae. *Plant Physiol* **114**: 631–6.

67. **Wooldridge SA.** 2009. A new conceptual model for the enhanced release of mucus in symbiotic reef corals during bleaching conditions. *Mar Ecol Prog Ser* **396**: 145–52.

68. **Borell EM**, **Bischof K.** 2008. Feeding sustains photosynthetic quantum yield of a scleractinian coral during thermal stress. *Oecologia* **157**: 593–601.

69. **Chen CA**, **Wang JT**, **Fang LS**, *et al*. 2005. Fluctuating algal symbiont communities in *Acropora palifera* (Scleractinia: Acroporidae) from Taiwan. *Mar Ecol Prog Ser* **295**: 113–21.

70. **Belda-Baillie CA**, **Baillie BK**, **Maruyama T.** 2002. Specificity of a model cnidarian-dinoflagellate symbiosis. *Biol Bull* **202**: 74–85.

71. **Frank SA.** 1996. Host-symbiont conflict over mixing of symbiotic lineages. *Proc R Soc Lond B* **263**: 339–44.

72. **Coles SL**, **Jokiel PL.** 1977. Effects of temperature on photosynthesis and respiration in hermatypic corals. *Mar Biol* **43**: 209–16.

73. **Al-Horani FA.** 2005. Effects of changing seawater temperature on photosynthesis and calcification in the scleractinian coral *Galaxea fascicularis*, measured with O_2, Ca^{2+} and pH microsensors. *Scientia Marina* **69**: 347–54.

74. **Berkelmans R**, **van Oppen MJH.** 2006. The role of zooxanthellae in the thermal tolerance of corals: a 'nugget of hope' for corals in an era of climate change. *Proc R Soc Lond B* **273**: 2305–12.

75. **Grottoli AG**, **Rodrigues LJ**, **Palardy JE.** 2006. Heterotrophic plasticity and resilience in bleached corals. *Nature* **440**: 1186–9.

76. **Ralph PJ**, **Gademann R**, **Larkum AWD.** 2001. Zooxanthellae expelled from bleached corals at 33 °C are photosynthetically competent. *Mar Ecol Prog Ser* **220**: 163–8.

77. **Steen RG**, **Muscatine L.** 1987. Low temperature evokes rapid exocytosis of symbiotic algae by a sea anemone. *Biol Bull* **172**: 246–63.

78. **Toller WW**, **Rowan R**, **Knowlton N.** 2001. Zooxanthellae of the *Montastraea annularis* species complex: patterns of distribution of four taxa of *Symbiodinium* on different reefs and across depths. *Biol Bull* **201**: 348–59.

79. **Ulstrup KE**, **van Oppen MJ.** 2006. Geographic and habitat partitioning of genetically distinct zooxanthellae (*Symbiodinium*) in *Acropora* corals on the Great Barrier Reef. *Mol Ecol* **23**: 3477–84.

80. **Ahmadjian V.** 1993. *The Lichen Symbiosis*. Hoboken: John Wiley and Sons.

81. **Hyvärinen M**, **Härdling R**, **Tuomi J.** 2002. Cyanobacterial lichen symbiosis: the fungal partner as an optimal harvester. *Oikos* **98**: 498–504.

82. **Combes C.** 2005. *The Art of Being a Parasite*. Chicago, USA: University of Chicago Press.

83. **Coffroth MA**, **Lewis C**, **Santos SR**, *et al*. 2006. Environmental populations of symbiotic dinoflagellates in the genus *Symbiodinium* can initiate symbioses with reef cnidarians. *Curr Biol* **16**: 985–7.

84. **Manning MM**, **Gates RD.** 2008. Diversity in populations of free-living *Symbiodinium* from a Caribbean and Pacific reef. *Limnol Oceanogr* **53**: 1853–61.

85. **Hirose M**, **Reimer JD**, **Hidaka M**, *et al*. 2008. Phylogenetic analyses of potentially free-living *Symbiodinium* spp. isolated from coral reef sand in Okinawa, Japan. *Mar Biol* **155**: 105–12.

86. **Pochon X**, **Stat M**, **Takabayashi M**, *et al*. 2010. Comparison of endosymbiotic and free-living *Symbiodinium* (Dinophyceae) diversity in a Hawaiian reef environment. *J Phycol* **46**: 53–65.

87. **Coffroth MA**, **Santos SR.** 2005. Genetic diversity of symbiotic dinoflagellates in the genus *Symbiodinium*. *Protist* **156**: 19–34.

88. **Piercey-Normore MD**, **DePriest PT.** 2001. Algal switching among lichen symbioses. *Am J Bot* **88**: 1490–8.

89. **Hoshina R**, **Imamura N.** 2008. Multiple origins of the symbioses in *Paramecium bursaria*. *Protist* **159**: 53–63.

90. **Stewart FJ**, **Young CR**, **Cavanaugh CM.** 2008. Lateral symbiont acquisition in a maternally transmitted chemosynthetic clam endosymbiosis. *Mol Biol Evol* **25**: 673–87.

91. **LaJeunesse TC.** 2004. 'Species' radiations of symbiotic dinoflagellates in the Atlantic and Indo-Pacific since the Miocene-Pliocene transition. *Mol Biol Evol* **22**: 570–81.

92. **Douglas AE**, **Smith DC.** 1989. Are endosymbioses mutualistic? *Trends Ecol Evol* **4**: 350–2.

93. **Mazancourt CD**, **Loreau M**, **Dieckmann U.** 2005. Understanding mutualism when there is adaptation to the partner. *J Ecol* **93**: 305–14.

94. **Scherf BD.** 2000. *World Watch List for Domestic Animal Diversity*, 3rd edition. Rome: FAO.

95. **Sunagawa S**, **Wilson EC**, **Thaler M**, *et al*. 2009. Generation and analysis of transcriptome resources on the rise: the sea anemone *Aiptasia pallida* and its dinoflagellate endosymbiont. *BMC Genomics* **10**: 258.

96. **Voolstra CR**, **Schwarz JA**, **Schnetzer J**, *et al*. 2009. The host transcriptome remains unaltered during the establishment of coral-algae symbioses. *Mol Ecol* **18**: 1823–33.

97. **Nishiguchi MK**, **Ruby EG**, **McFall-Ngai MJ.** 1998. Competitive dominance among strains of luminous bacteria provides an unusual form of evidence for parallel evolution in sepiolid squid-vibrio symbioses. *Appl Environ Microbiol* **64**: 3209–13.

98. **Chun CK**, **Troll JV**, **Koroleva I**, *et al*. 2008. Effects of colonisation, luminescence, and autoinducer on host transcription during development of the squid-vibrio association. *Proc Nat Acad Sci (USA)* **105**: 11323–8.

99. **Desalvo MK**, **Voolstra CR**, **Sunagawa S**, *et al*. 2008. Differential gene expression during thermal stress and bleaching in the Caribbean coral *Montastraea faveolata*. *Mol Ecol* **17**: 3952–71.

100. **Coles SL**, **Jokiel PL.** 1978. Synergistic effects of temperature, salinity and light on the hermatypic coral *Montipora verrucosa*. *Mar Biol* **49**: 187–95.

101. **Brown BE**, **Dunne RP**, **Goodson MS**, *et al*. 2002. Experience shapes the susceptibility of a reef coral to bleaching. *Coral Reefs* **21**: 119–26.

102. **Ulstrup KE**, **Berkelmans R**, **Ralph PJ**, *et al*. 2006. Variation in bleaching sensitivity of two coral species across a latitudinal gradient on the Great Barrier Reef: the role of zooxanthellae. *Mar Ecol Prog Ser* **314**: 135–48.

103. **Berkelmans R**, **Willis BL.** 1999. Seasonal and local spatial patterns in the upper thermal limits of corals on the inshore Central Great Barrier Reef. *Coral Reefs* **3**: 219–28.

104. **Fagoonee I**, **Wilson HB**, **Hassell MP**, *et al*. 1999. The dynamics of zooxanthellae populations: a long-term study in the field. *Science* **283**: 843–5.

105. **Wooldridge SA**, **Done TJ.** 2009. Improved water quality can ameliorate effects of climate change on corals. *Ecol Appl* **19**: 1492–9.

106. **Wooldridge SA.** 2009. Water quality and coral bleaching thresholds: Formalising the linkage for the inshore reefs of the Great Barrier Reef, Australia. *Mar Poll Bull* **58**: 745–51.

107. **Makkonen A**, **Hurri RSK**, **Hyvärinen M.** 2007. Differential responses of lichen symbionts to enhanced nitrogen and phosphorus availability: An experiment with *Cladina stellaris*. *Ann Bot* **99**: 877–84.

108. **Neckelmann N**, **Muscatine L.** 1983. Regulatory mechanisms maintaining the *Hydra-Chlorella* symbiosis. *Proc R Soc Lond Ser B* **219**: 193–210.

109. **Genin A**, **Lazar B**, **Brenner S.** 1995. Vertical mixing and coral death in the Red-Sea following the eruption of mount-Pinatubo. *Nature* **377**: 507–10.

110. **Pochon X**, **Montoya-Burgos JI**, **Stadelmann B**, *et al*. 2006. Molecular phylogeny, evolutionary rates, and divergence timing of the symbiotic dinoflagellate genus *Symbiodinium*. *Mol Phylogenet Evol* **38**: 20–30.

111. **Zachos J**, **Pagani M**, **Sloan L**, *et al*. 2001. Trends, rhythms and aberrations in global climate 65 Ma to present. *Science* **292**: 686–93.

112. **Pomar L**, **Hallock P.** 2007. Changes in coral-reef structure through the Miocene in the Mediterranean province: Adaptive *versus* environmental influence. *Geology* **35**: 899–902.

Review essays