



A hypothesis linking sub-optimal seawater $p\text{CO}_2$ conditions for cnidarian-*Symbiodinium* symbioses with the exceedence of the interglacial threshold (>260 ppmv)

S. A. Wooldridge

Australian Institute of Marine Science, PMB #3, Townsville MC, QLD, 4810, Australia

Correspondence to: S. A. Wooldridge (s.wooldridge@aims.gov.au)

Received: 26 September 2011 – Published in Biogeosciences Discuss.: 23 November 2011

Revised: 22 March 2012 – Accepted: 25 April 2012 – Published: 15 May 2012

Abstract. Most scleractinian corals and many other cnidarians host intracellular photosynthetic dinoflagellate symbionts (“zooxanthellae”). The zooxanthellae contribute to host metabolism and skeletogenesis to such an extent that this symbiosis is well recognised for its contribution in creating the coral reef ecosystem. The stable functioning of cnidarian symbioses is however dependent upon the host’s ability to maintain demographic control of its algal partner. In this review, I explain how the modern envelope of seawater conditions found within many coral reef ecosystems (characterised by elevated temperatures, rising $p\text{CO}_2$, and enriched nutrient levels) are antagonistic toward the dominant host processes that restrict excessive symbiont proliferation. Moreover, I outline a new hypothesis and initial evidence base, which support the suggestion that the additional “excess” zooxanthellae fraction permitted by seawater $p\text{CO}_2$ levels beyond 260 ppmv significantly increases the propensity for symbiosis breakdown (“bleaching”) in response to temperature and irradiance extremes. The relevance of this biological threshold is discussed in terms of historical reef extinction events, glacial-interglacial climate cycles and the modern decline of coral reef ecosystems.

able changes in the surface ocean carbonate system, including a decrease in carbonate ion concentration [CO_3^{2-}] and pH (Fig. 1). This so-called “ocean acidification” reduces the degree of oversaturation with respect to the precipitation of calcium carbonate (CaCO_3). The great fear of many scientists is that suboptimal saturation states will affect the calcification process of marine calcifying organisms, with potential negative consequences for many marine ecosystems including coral reefs (reviewed by Kleypas and Langdon, 2006).

Arguably of more immediate concern, however, is the growing speculation that increasing seawater $p\text{CO}_2$ may also act to destabilise the ecologically important relationship between reef-building cnidarians (e.g. corals) and their symbiotic dinoflagellates (Pecheux, 2002; Ravindran and Raghukumar, 2006; Anthony et al., 2008). In this review, I consider the possible physiological basis for $p\text{CO}_2$ -driven instability of cnidarian symbioses. I begin by outlining how increasing [$\text{CO}_{2(\text{aq})}$] in conjunction with nutrient-replete conditions can disrupt the host’s ability to maintain demographic control of its algal partner. Moreover, I provide evidence to support the suggestion that the “excess” of algal symbionts permitted by seawater $p\text{CO}_2$ levels beyond 260 ppmv significantly increases the propensity for symbiosis breakdown (“bleaching”) in response to irradiance and temperature extremes. The relevance of this biological threshold is discussed in terms of historical reef extinction events, glacial-interglacial climate cycles and the modern decline of coral reef ecosystems. In concluding, I argue that the $p\text{CO}_2$ -dependent construct for the causes and consequences of bleaching reveals a new level of determinism behind the

1 Introduction

Due to rapid air-sea gas exchange, the observed past and predicted future rise in atmospheric carbon dioxide (CO_2) partial pressure ($p\text{CO}_2$) causes a corresponding increase in dissolved seawater $\text{CO}_{2(\text{aq})}$ concentrations in upper ocean waters (Najjar, 1992). Increasing [$\text{CO}_{2(\text{aq})}$] leads to consider-

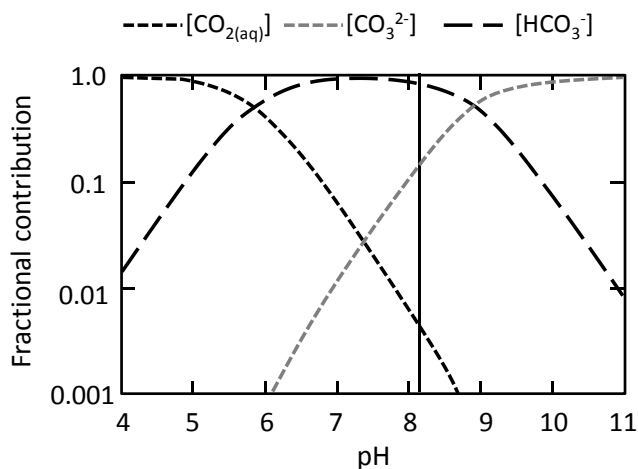


Fig. 1. Bjerrum plot showing the relative contributions of $\text{CO}_2(\text{aq})$, bicarbonate (HCO_3^-) and carbonate (CO_3^{2-}) ions to total dissolved inorganic carbon (DIC) as a function of pH. Present day seawater has a pH of approximately 8.1 and is therefore dominated by HCO_3^- .

characteristic dynamics (and drivers) of the coupled land-ocean-atmosphere carbon cycle of the Earth System.

2 Background: the cnidarian-*Symbiodinium* symbiosis

The high productivity and extensive accretion of skeletal CaCO_3 by shallow-water tropical reef ecosystems is testament to the evolutionary success of the symbiotic association between scleractinian (“reef-building”) corals and unicellular dinoflagellate algae of the genus *Symbiodinium* (“zooxanthellae”) (Fig. 2a; Veron, 1995; Stanley, 2006). Within this association, the zooxanthellae live within the coral tissues in extremely high densities (greater than 10^6 cm^{-2}) and perform intensive photosynthesis (Fig. 1a). Under the optimal conditions provided by nutrient-poor tropical waters, the vast majority (>90 %) of this assimilated organic carbon (“photosynthate”) is typically translocated to the coral, contributing substantially to its carbon and energy needs (Fig. 2b; Trench, 1993; Yellowlees et al., 2008). Scleractinian corals are not the only hosts to *Symbiodinium* – a number of other cnidarians host symbiotic dinoflagellates (octocorals, sea anemones, zoanthids, scyphozoan, and hydrozoans) (Muller-Parker and Davy, 2001), as well as a number of other invertebrates and protists. However, by far the most common host to dinoflagellates are the cnidarians, particularly tropical species.

Traditionally, the “producer-within-consumer” arrangement of the cnidarian-*Symbiodinium* symbiosis has been heralded as the epitome of mutual cooperation (reviewed by Trench, 1993; Yellowlees et al., 2008). This view is blurred by the proposed role of the host as an active “farmer” of the energy-rich photosynthate from its demographically-controlled algal partner (Wooldridge, 2010). Such host ma-

nipulation is achieved by evolved strategies that endeavour to control the intracellular supply of essential substrates needed for zooxanthellae growth and photosynthesis – principally $\text{CO}_2(\text{aq})$ and dissolved inorganic nitrogen (DIN = ammonium + nitrate + nitrite). However, as explained in greater detail below, external (seawater) enrichment of these essential substrates can render ineffective the host’s control strategies, and permit rapid proliferation of the zooxanthellae population. Far from being beneficial, an enlarged zooxanthellae population is predicted to become a metabolic burden to the coral host during periods of high irradiance and temperature, leading to the deleterious onset of intracellular CO_2 -limitation and zooxanthellae expulsion (= coral bleaching) (Fig. 2c; Wooldridge, 2009a, 2010). Recent observations from the “bleaching-sensitive” La Saline reef (La Réunion Island, western Indian Ocean; Naim, 1993) demonstrate the plausible nature of this breakdown sequence. At this reef site, nutrient-enriched groundwater discharge (mainly nitrate) supports an enlarged (~3 times) zooxanthellae population that is CO_2 -limited even at normal (ambient) irradiance levels (Chauvin et al., 2011).

Before considering the extent to which the current (and emerging) envelope of seawater conditions may be antagonistic toward the dominant host processes that restrict excessive symbiont proliferation, it is beneficial to first consider the environmental conditions that are predicted by Wooldridge (2009a, 2010) to be most optimal for a stable (host-controlled) symbiosis, i.e. a symbiosis in which the intracellular zooxanthellae are heavily reliant upon a host supply of $\text{CO}_2(\text{aq})$ and DIN. In terms of the intracellular (symbiotic) supply of $\text{CO}_2(\text{aq})$, the host maintains optimal control when the “passive” seawater supply of $\text{CO}_2(\text{aq})$ is severely limiting such that the photosynthetic activities (= CO_2 demand) of the zooxanthellae population is heavily reliant upon the energy-dependent (“active”) host CO_2 -concentrating mechanisms (CCMs) (Fig. 3). The linkage of these CCMs to the receipt of photosynthate ensures that the zooxanthellae indirectly play a role in generating the $\text{CO}_2(\text{aq})$ that they themselves require for photosynthesis; thus representing 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.

At a gross population level, the maximum host-controlled zooxanthellae density should also be optimally matched to the prevailing autotrophic capacity. Notably, in both tropical and temperate cnidarians, the maximum transfer of photosynthate by the zooxanthellae population reaches a *density-dependent* limit, such that transfer rates are lowest at both very low zooxanthellae densities (due to low densities per se) and very high zooxanthellae densities (due to low per capita rates) (Fig. 4; Anthony et al., 2009; Hoogenboom et al., 2010). The considered impact of an enlarged zooxanthellae

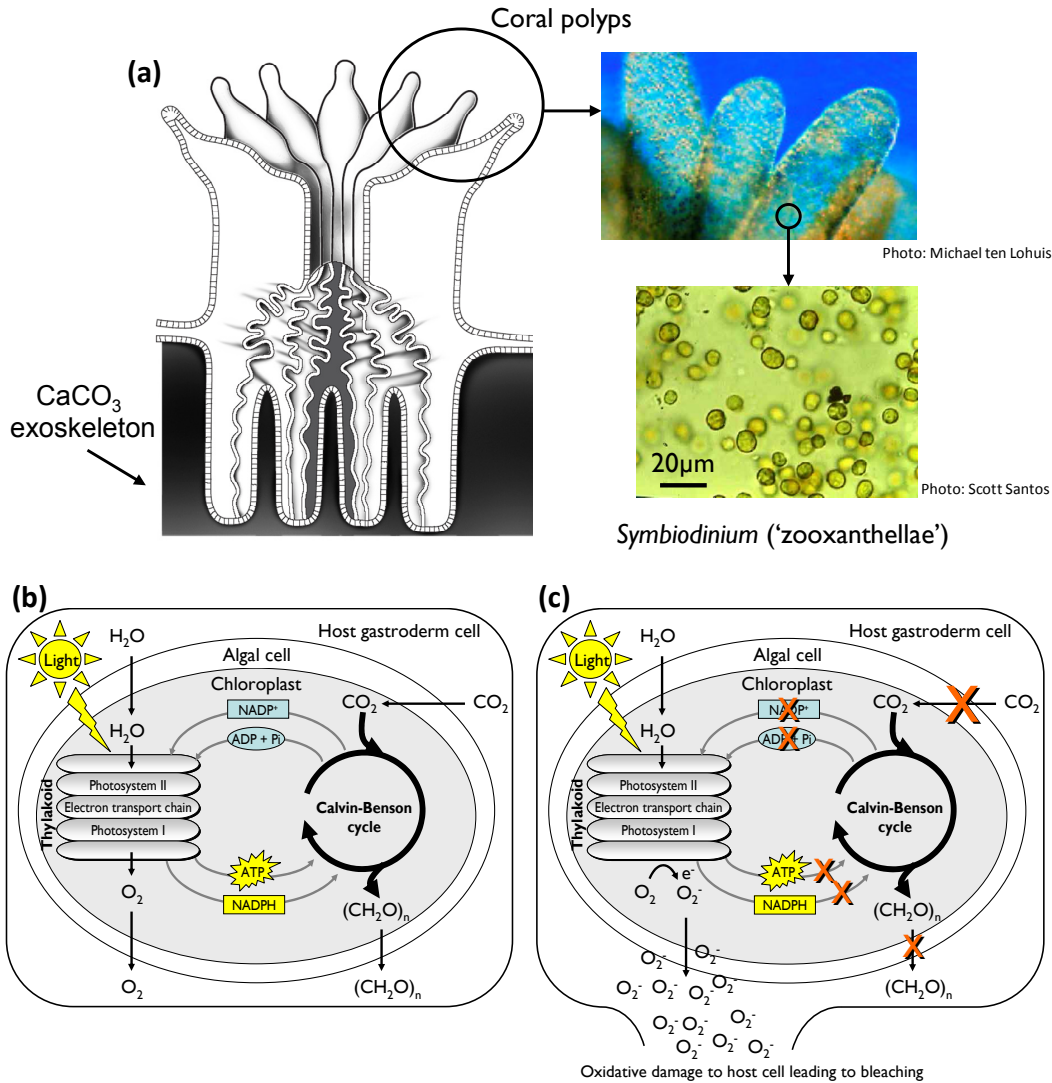


Fig. 2. The coral-algae endosymbiosis. **(a)** A reef coral is a symbiotic association between an animal (the host) and unicellular dinoflagellate algae (the symbiont). Within this association, the dinoflagellate algae of the genus *Symbiodinium* (“zooxanthellae”) reside within the gastrodermal cells of the coral host. **(b)** Zooxanthellae photosynthesis takes place within the algae chloroplast, with the “light” reactions occurring in the thylakoid membranes and the “dark” reactions (Calvin-Benson cycle) in the stroma. The vast majority (>90 %) of the assimilated photosynthate $(\text{CH}_2\text{O})_n$ is typically transferred to the coral host. **(c)** Intracellular limitation of CO_2 for the “dark reactions” of zooxanthellae photosynthesis is proposed to trigger a breakdown of the symbiosis (= zooxanthellae expulsion) (Wooldridge, 2009a, 2010). With no means to turn over ATP and NADPH, the photosynthetic electron transport chain becomes blocked, which damages the light-sensitive photosystems and generates membrane damaging reactive oxygen species.

density on the stability and functioning of the host CCMs helps in explaining this response. In this case, as densities increase, the photosynthetic capacity per zooxanthella (P) progressively *decreases* (possibly due to increased self-shading and/or CO_2 -limitation within the host cell) whilst the associated respiratory/maintenance cost to the symbiosis (R) *increases* (linearly) per zooxanthella added (Anthony et al., 2009; Hoogenboom et al., 2010). In this way, it is understood that there exists an optimum zooxanthellae density that maximises autotrophic capacity ($P:R$), i.e. every zoox-

anthella added beyond this optimum reduces the autotrophic energy (ATP) transferred to the coral host. Similarly, the maximum efficiency of the ATP-dependent CCMs will be linked to this optimum zooxanthellae density, i.e. every zooxanthella added beyond the optimum reduces the efficiency of the host CCMs. Notably, the standing stock of zooxanthellae within both tropical and temperate corals can be more than double the predicted optimum zooxanthellae density (Fig. 4; Anthony et al., 2009; Hoogenboom et al., 2010). This reveals two crucial details about the modern coral-algae symbiosis:

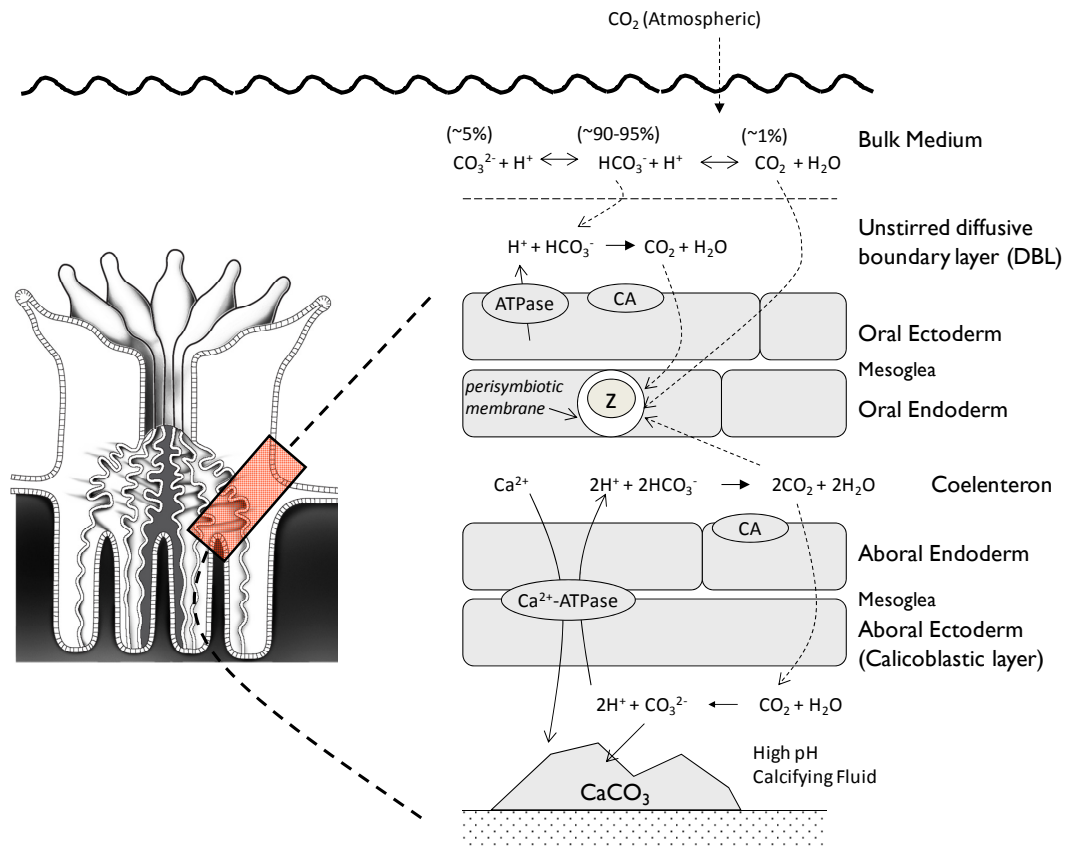


Fig. 3. Active and passive seawater $\text{CO}_2(\text{aq})$ supply pathways for the intracellular zooxanthellae within the coral symbiosis. Whilst respiratory $\text{CO}_2(\text{aq})$ is available from both zooxanthellae and animal pathways, it accounts for only $\sim 50\%$ of the carbon needed by the algae during high rates of photosynthesis (Muscatine et al., 1989). High rates of photosynthesis thus place strong (additional) demands upon a seawater supply of $\text{CO}_2(\text{aq})$. Although seawater $\text{CO}_2(\text{aq})$ can passively diffuse across the lipid bilayer of the host, at typical seawater pH (8.1) it represents only a small fraction ($\sim 1\%$) of the dissolved inorganic carbon (DIC) available from seawater. The much more abundant HCO_3^- , however, is largely inhibited from diffusing into the host cells due to its ionic charge. To enhance the intracellular supply of $\text{CO}_2(\text{aq})$ for its zooxanthellae (Z), the coral host maintains a range of active “ CO_2 -concentrating mechanisms” (CCMs). The CCMs utilise metabolic energy in the form of adenosine triphosphate (ATP) to convert seawater HCO_3^- into readily diffusible $\text{CO}_2(\text{aq})$. For example, at the ectodermal surface, hydration of HCO_3^- to $\text{CO}_2(\text{aq})$ is achieved via a H^+ -ATPase enzyme in combination with carbonic anhydrase (CA) (Furla et al., 2000; Al Horani et al., 2003a). Similarly, by functioning to increase the availability of $\text{CO}_2(\text{aq})$ within the coelenteron, the Ca^{2+} -ATPase enzyme that underpins host skeletal accretion also represents an important energy-driven CCM (McConnaughey and Whelan, 1997; Al Horani et al., 2003b). The ATP needed to activate the CCMs is ultimately derived from the autotrophic carbon products of the zooxanthellae (Al Horani et al., 2003b).

(i) under ambient (benign) conditions, the loss in autotrophic capacity per zooxanthella added beyond the optimum density must be relatively small, thus permitting large changes in zooxanthellae densities to occur between $(\text{P}:\text{R})_{\text{optimum}}$ and the symbiosis breakpoint where autotrophic capacity is completely lost ($\text{P}:\text{R} < 1$), and (ii) the addition of “excess” zooxanthellae beyond the optimum, determined by the transport rate and capacity of the host CCMs, must be primarily facilitated by the passive diffusion of seawater $\text{CO}_2(\text{aq})$ and not the active (ATP-dependent) dehydration of seawater HCO_3^- .

Historically, such post-mitotic population control by the coral host would have benefited from the extremely low seawater concentration of $\text{CO}_2(\text{aq})$ (Fig. 1). Seawater $\text{CO}_2(\text{aq})$ is transferred between the host and the surrounding wa-

ter via diffusion, with this diffusive flux being inversely proportional to the boundary layer thickness and directly proportional to the bulk seawater $\text{CO}_2(\text{aq})$ concentration (Denny, 1988). Despite representing only a small component ($\sim 1\%$) of the available seawater DIC at present seawater pH (8.1), $[\text{CO}_2(\text{aq})]$ has none-the-less risen 50–100% since the early 1800s ($p\text{CO}_2 \sim 280$ ppmv) and present day ($p\text{CO}_2 \sim 390$ ppmv), and is projected to represent an $\sim 200\%$ increase by 2100 ($p\text{CO}_2 \sim 750$ ppmv) (Wolf-Gladrow et al., 1999). The potentially disruptive influence of this enhanced “passive” supply of $\text{CO}_2(\text{aq})$ on the stable functioning of cnidarian symbioses should not be understated, since it provides the opportunity for an increasing (“excess”) proportion of the zooxanthellae population to exist beyond the biophysical

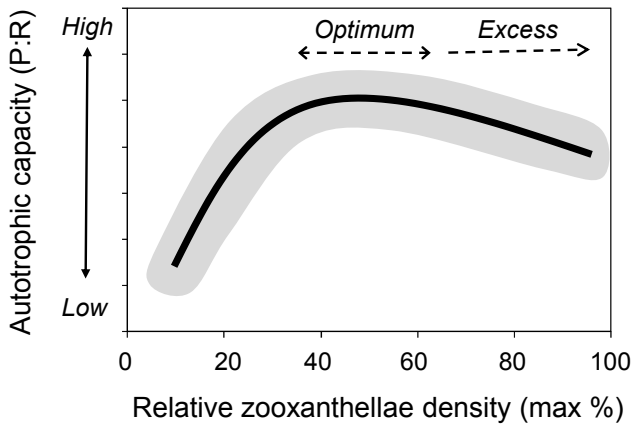


Fig. 4. Schematic representation of the optimal zooxanthellae density range in terms of autotrophic capacity (P:R). The relationship is consistent with physiological measurements taken from both a tropical and temperate coral (Anthony et al., 2009; Hoogenboom et al., 2010).

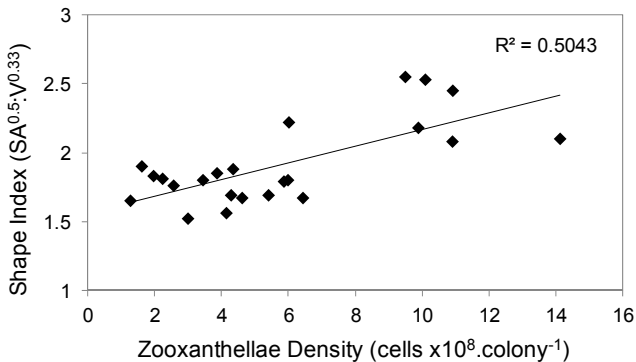


Fig. 5. Variation in zooxanthellae densities based on different shaped colonies of *Montastrea annularis* (after Patterson et al., 1991). Zooxanthellae counts (per colony) are linked to a dimensionless shape index (surface area^{0.5}:displacement volume^{0.33}). More diffusive colony shapes (= larger shape index) tend to have higher zooxanthellae densities.

optimum imposed by the photosynthate-feedback operation of the CCMs.

Experimental observations confirm the potential sensitivity of the in hospite symbiont population to rising seawater $p\text{CO}_2$. For example, increasing $p\text{CO}_2$ from 400 to 700 ppmv during low ambient irradiance (winter) conditions resulted in a doubling of the number of zooxanthellae within the temperate coral *Cladocora caespitosa* (Rodolfo-Metalpa et al., 2010). Operationally, the “excess” zooxanthellae increase the gross size of the symbiont population, principally via an increased number of zooxanthellae inside each host gastroderm cell (the so-called cell-specific density, CSD). For example, an experimental increase of seawater $p\text{CO}_2$ from 460–760 ppmv under moderate ($380 \mu\text{mol photon m}^{-2} \text{s}^{-1}$) irradiance levels increased the CSD of *Stylophora pistil-*

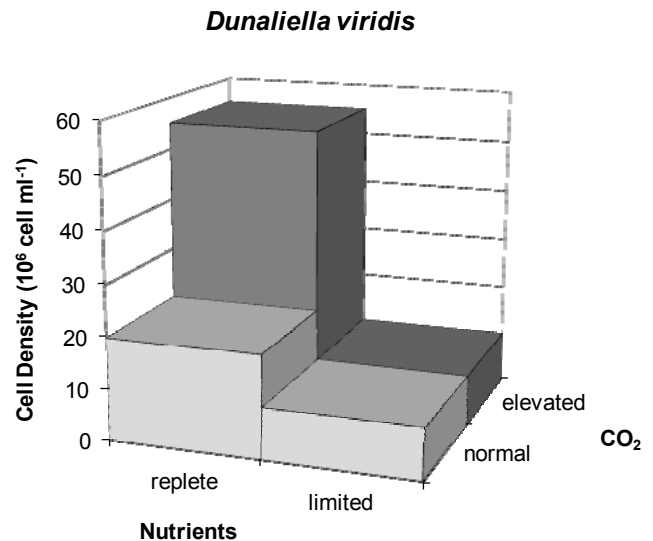


Fig. 6. Cell densities of *Dunaliella viridis* batch cultured under normal air (0.035% CO_2) and CO_2 -enriched air (1% CO_2) in nitrogen-sufficient and nitrogen-limited conditions (after Gordillo et al., 2003). Elevated CO_2 conditions act to increase cell densities only under conditions of NH_4^+ sufficiency.

lata from 1.3 to 1.7 (Reynaud et al., 2003), i.e. in the high $p\text{CO}_2$ treatment, 52% of host gastroderm cells contained two or more zooxanthellae, compared with 30% in the lower $p\text{CO}_2$ treatment. Additional factors that reduce the thickness of the diffusive boundary layer, such as high flow rates and/or “branching” coral morphologies with high mass transfer rates (i.e. high surface area: volume ratios) also permit enhanced zooxanthellae densities and CSD (Fig. 5; Patterson et al., 1991; Helmuth et al., 1997; Muscatine et al., 1998; Nakamura et al., 2003; Strychar et al., 2004; Mass and Genin, 2008).

The *realised* size of the “excess” zooxanthellae population may be restricted by the intracellular availability of essential nutrients needed for algal cell division (e.g. NH_4^+). By analogy, this constraint is demonstrated by the growth dynamics of the free-living unicellular alga *Dunaliella viridis* when subject to external seawater manipulations of $\text{CO}_{2(\text{aq})}$ and NH_4^+ (Fig. 6; Gordillo et al., 2003). In this case, elevated $\text{CO}_{2(\text{aq})}$ acts to increase algae cell densities *only* under conditions of NH_4^+ sufficiency. The typical increase in zooxanthellae densities and CSD in cnidarians hosts when exposed to seawater enriched with DIN (Stimson and Kinzie, 1991; Muscatine et al., 1998; Ferrier-Pagès et al., 2001) suggests that zooxanthellae growth is often nutrient-limited in hospite, be it due to low (ambient) seawater DIN concentrations and/or active host constraint mechanisms. Growth-limiting conditions compel the zooxanthellae to transfer the bulk of their assimilated photosynthate to the host, even under elevated $p\text{CO}_2$ conditions (Dubinsky and Jokiel, 1994; Dubinsky and Berman-Frank, 2001).

Under nutrient-replete conditions, the maximum size of the “excess” zooxanthellae fraction is predicted to balance around the dynamic interplay between the supply and demand for readily-diffusible seawater $\text{CO}_{2(\text{aq})}$ (Wooldridge, 2009a, 2010). In non-upwelling areas, the bulk concentration (supply) of seawater $\text{CO}_{2(\text{aq})}$ is relatively stable on timescales less than 1 year (Kawahata et al., 1997). However, the photosynthetic demand (zooxanthella^{-1}) for seawater $\text{CO}_{2(\text{aq})}$ varies dynamically with the integrated (daily + seasonal) pattern of photosynthetic active radiation (PAR) (Muscatine et al., 1989). As such, reduced PAR typical of the cooler winter-spring seasons may permit a larger “excess” zooxanthellae fraction than the high PAR conditions typical of summer. This irradiance-driven competition for $\text{CO}_{2(\text{aq})}$ is consistent with the inverse relationship between zooxanthellae densities and seasonal irradiance levels, which exists even in non-bleaching years (Stimson, 1997; Fitt et al., 2000). Moreover, it alludes to the potential onset of intracellular CO_2 -limitation (= zooxanthellae expulsion; Fig. 2c) on a continuous (daily) basis during the high photon flux period around midday, especially for nutrient-replete conditions (Stimson and Kinzie, 1991; Jones and Yellowlees, 1997). Although under ambient (benign) temperature and irradiance conditions this daily turnover of zooxanthellae represents only 1–2% of the total zooxanthellae standing stock (Stimson and Kinzie, 1991; Jones and Yellowlees, 1997), as temperatures and irradiances approach anomalous maxima, the turnover rate can increase towards 50%, especially in high mass-transfer (branching) species (Strychar et al., 2004).

In terms of the carbon (i.e. energy) balance of the symbiosis, the growth rate of the remnant zooxanthellae (“mitotic index”, MI) is a crucial parameter for understanding whether this daily expulsion dynamic represents a significant carbon sink. For as long as the improved photosynthetic performance of the remaining zooxanthellae (P) exceeds the respiratory cost of the regrowth and cell maintenance (R), then a net positive autotrophic carbon balance ($P:R > 1$) may result across the diurnal cycle. The problem arises during classic “bleaching conditions”, wherein periods of extreme irradiance (= large number zooxanthellae expelled day^{-1}) are coupled with warm seawater conditions that favour rapid regrowth (day^{-1}) from the remnant zooxanthellae (Bhagooli and Hidaka, 2002; Strychar et al., 2004). In this case, although P_{MAX} may even remain stable, the high respiratory cost of regrowth can lead to a negative autotrophic carbon balance ($P:R < 1$), wherein more carbon per day is directed into new cell production than is transferred to the host (Verde and McCloskey, 1996). This negative relationship between excessive symbiont MI and photosynthate transfer and has been documented in corals, sea-anemones and jellyfish (Verde and McCloskey, 1996; McGuire and Szmant, 1997; Sachs and Wilcox, 2006). Significantly, an extended (several days–weeks) run of diminished autotrophic capacity is proposed to underpin a self-enhancing disruption (cessation) of the ATP-dependent host CCMs – leading to the *mass* ex-

pulsion of the bulk zooxanthellae complement (Wooldridge, 2009a, 2010).

This CCM disruption \rightarrow CO_2 -limitation bleaching model (sensu Wooldridge, 2009a, 2010) reveals a subtle paradox for the cnidarian-*Symbiodinium* symbiosis, namely an enhanced susceptibility to intracellular CO_2 -limitation (and subsequent zooxanthellae expulsion) as seawater $p\text{CO}_2$ increases. As alluded, this paradox is ultimately linked to the increased permitted size of the “excess” zooxanthellae fraction that functions on the passive supply route of seawater $\text{CO}_{2(\text{aq})}$, and which is extremely vulnerable to CO_2 -limitation during periods of excessive (irradiance-driven) $\text{CO}_{2(\text{aq})}$ demand; particularly when coupled with a flow-mediated reduction in passive $\text{CO}_{2(\text{aq})}$ supply, which is a characteristic feature of the “doldrum” conditions that normally precede *mass* bleaching events (Gleason and Wellington, 1993). The CCM disruption \rightarrow CO_2 -limitation bleaching model also permits a rough estimate of the present-day size of the “excess” zooxanthellae fraction, since although being the potential triggering-agent for the bulk loss of the CCM-dependent zooxanthellae fraction, a passive $\text{CO}_{2(\text{aq})}$ -dependent fraction should recover (persist) even in severely bleached animals, despite being of limited caloric importance (Wooldridge, 2009a). Indeed, severely bleached corals still retain >10–30% of their zooxanthellae complement, depending on prevailing irradiance, flow and morphological considerations (see e.g. Hoegh-Guldberg and Smith, 1989; Berkelmans and Willis, 1999; Okamoto et al., 2005). A significant portion of this >10–30% is potentially representative of the “excess” zooxanthellae fraction that is permitted by the passive supply of seawater $\text{CO}_{2(\text{aq})}$, especially since the contributing supply source of respiratory $\text{CO}_{2(\text{aq})}$ is severely restricted immediately following a bleaching event (Porter et al., 1989).

An important corollary to the suggested sensitivity of the modern cnidarian-*Symbiodinium* symbiosis to rising seawater $p\text{CO}_2$, is the existence of a $p\text{CO}_2$ threshold below which the permitted size of the “excess” fraction is too small to trigger physiological disruption (“bleaching”), even during periods of elevated irradiance and temperature. In this review, I integrate existing biological and geological data sets to propose that this $p\text{CO}_2$ threshold exists ~ 260 ppmv – well below the present day $p\text{CO}_2 \sim 390$ ppmv.

3 Biological evidence of symbiosis disruption beyond $p\text{CO}_2 = 260$ ppmv

3.1 Increased turnover and loss of zooxanthellae

A number of studies have noted an increased sensitivity to bleaching under high $p\text{CO}_2$ conditions (Pecheux, 2002; Ravindran and Raghukumar, 2006; Anthony et al., 2008). Several other studies have recorded no apparent changes in sensitivity (see e.g. Rodolfo-Metalpa et al., 2010). An integrated picture emerges for the underpinning sequence of

disruption in the experiments that do record an increased turnover and loss of zooxanthellae. Firstly, disruption in the photosynthetic processes (i.e. decrease photosynthetic yield) of the zooxanthellae precedes their expulsion (Pecheux, 2002). Secondly, despite their reduced numbers, the remnant zooxanthellae have elevated MI, suggestive of uncontrolled division (Ravindran and Raghukumar, 2006). Most notably, coral bleaching extrapolations obtained via the joint manipulation of seawater temperatures and $p\text{CO}_2$ highlight the apparent significance of exceeding the ~ 260 ppmv threshold in terms of zooxanthellae turnover and loss (Fig. 7; Anthony et al., 2008). Indeed, the projected trends indicate that irrespective of temperature or morphology, a fundamental (pre-conditioning) trigger for zooxanthellae loss is the exceedence of $p\text{CO}_2$ beyond ~ 260 ppmv. Significantly, the tank treatments were carried out under high summer irradiance ($700\text{--}1000 \mu\text{mol photon m}^{-2} \text{s}^{-1}$) and with a nutrient-replete lagoonal seawater source (Hoegh-Guldberg et al., 2004).

The experimental findings are therefore consistent with the proposed importance of high irradiance and nutrient-replete conditions as *conditional* components for the observed enhancement of thermal bleaching under elevated $p\text{CO}_2$ conditions. Moreover, the nature of these results do not discount the proposed bleaching mechanism outlined here, whereby for seawater $p\text{CO}_2 < 260$ ppmv, the permitted size of the “excess” zooxanthellae fraction (supported by diffusive seawater $\text{CO}_{2(\text{aq})}$) is too small to be capable of disrupting the stable functioning of the bulk zooxanthellae fraction (supported by the host CCMs), even at presently accepted upper (synergistic) limits for temperature, irradiance, nutrient status, and coral morphology. Whilst, for $p\text{CO}_2 > 260$ ppmv the well-described modern bleaching characteristics emerge, namely: (i) increased bleaching susceptibility at higher temperatures, driven by a progressive decline in autotrophic capacity (P:R) (see e.g. Coles and Jokiel, 1977), and (ii) enhanced zooxanthellae turnover and loss within coral species with high mass transfer morphologies (i.e. branching and plating) (Marshall and Baird, 2000; Loya et al., 2001; Grimsditch et al., 2008).

The logic follows, that for modern seawater conditions ($p\text{CO}_2 > 260$ ppmv) whole-colony bleaching represents the destructive endpoint to a suite of cellular processes that can operate near continuously in cnidarian symbioses. Perhaps the most visible, but previously unconnected indication of this phenomenon, are the zooxanthellae-free “white tips” on branching corals, and “white edges” on plating corals (Oliver, 1984). The tips and edges of corals represent sites of maximal mass transfer for diffusive substrates such as DIN and $\text{CO}_{2(\text{aq})}$ (Helmuth et al., 1997). Here, the low zooxanthellae density *but* high MI (Fang et al., 1989; Jones and Yellowlees, 1997) is consistent with the near continuous operation of irradiance-driven zooxanthellae turnover and loss, even at normal ambient temperatures (see e.g. Yamashita et al., 2011). This observation aligns with the emergent bleaching patterns from more extreme thermal stress, which also proceed from high mass transfer regions (tips and edges)

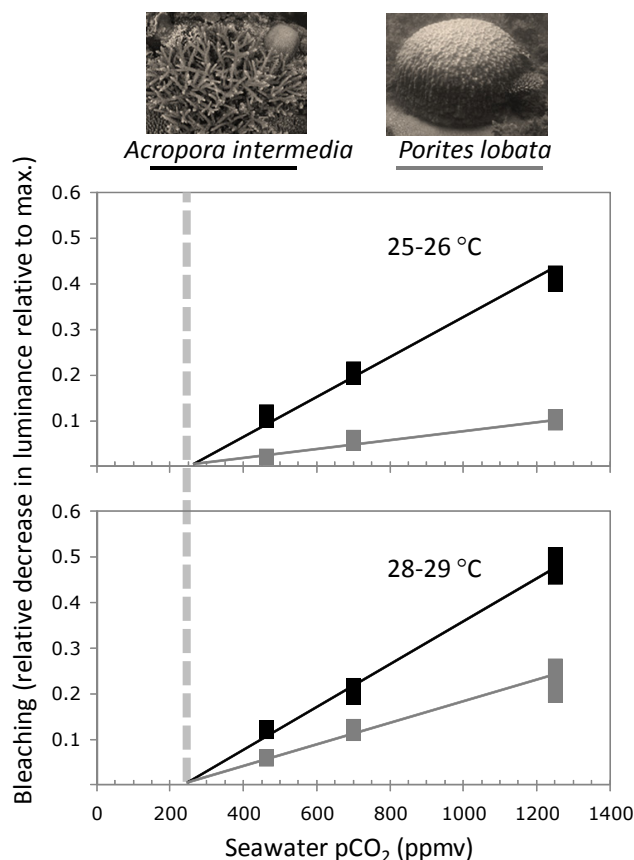


Fig. 7. Coral bleaching projections based on experimental manipulation of seawater temperatures and $p\text{CO}_2$ (after Anthony et al., 2008). The treatments were carried out under extremely high summer irradiance ($\sim 1000 \mu\text{mol photon m}^{-2} \text{s}^{-1}$) and with a nutrient-replete lagoonal seawater source. Comparative trends are shown for *Acropora intermedia* (branching morphology) and *Porites lobata* (massive/robust morphology). The error-bounded bleaching trends suggest that minimal bleaching will be observed for seawater $p\text{CO}_2 < 260$ ppmv, even at presently accepted upper (synergistic) limits for temperature, irradiance, nutrient status, and coral morphology.

towards lower mass transfer regions (base and centre) (see e.g. Shenkar et al., 2005). In the same way, corals located in natural high flow habitats are often more sensitive to thermal bleaching (see e.g. McClanahan et al., 2005; Carpenter and Patterson, 2007). The apparent conflicting evidence provided by short-term laboratory experiments, in which increased water flow reduces photoinhibition and improves the photosynthetic capacity of endosymbionts (see e.g. Nakamura et al., 2005) can be rationalised by a failure to allow sufficient time (days–several weeks), and/or provide access to the necessary inorganic nutrients (e.g. NH_4^+) needed to establish the flow-enlarged (CO_2 -equilibrating) density before the onset of thermal stress. For these laboratory situations, the increased flow condition is experienced as an effective

increase in CO_2 per zooxanthella, which is quite different from the predicted field situation.

The present-day exceedence of seawater $p\text{CO}_2$ beyond 260 ppmv also identifies the now crucial importance of nutrient-status for defining thermal bleaching sensitivity. It is thus consistent that reef areas with high nutrient availability (whether due to terrestrial runoff or deep ocean upwelling) are characterised by lower bleaching thresholds and more severe bleaching impacts (D’Croz et al., 2001; Wooldridge, 2009a; Wooldridge and Done, 2009; Wagner et al., 2010). Indeed, a unifying feature from world-wide reef locations that exhibit high ($>33^\circ\text{C}$) bleaching thresholds is their strongly oligotrophic surface waters during the warm summer months (e.g. Red Sea – no summer river runoff (Genin et al., 1995), Western Pacific Warm Pool – restricted upwelling due to strong thermal stratification (Tomczak and Godfrey, 1994), Northern Australia – low nutrient loads in summer river runoff (Wooldridge, 2009b).

3.2 Reduced calcification (=reduced activity of host CCMs)

Numerous studies demonstrate the negative impact of increased seawater $p\text{CO}_2$ on the calcification process of cnidarians, particularly symbiotic corals (reviewed by Kleypas and Langdon, 2006). In addition to the detrimental geochemical consequences of rising $p\text{CO}_2$ (Kleypas et al., 1999) the potential for autotrophic disruption in cnidarian-*Symbiodinium* symbioses when seawater $p\text{CO}_2$ exceeds 260 ppmv contributes an additional biological response mechanism with which to understand the negative impact of increased seawater $p\text{CO}_2$ on coral calcification. Specifically, disruption to the energy-dependent enzyme Ca^{2+} -ATPase, and its linked impact on host calcification and intracellular CO_2 supply (Fig. 3). Beyond the enhanced susceptibility of symbiotic corals to the impacts of ocean acidification (Cohen and Holcomb, 2009), several factors identify the host CCM-calcification linkage as a potential source of vulnerability. Firstly, given the paradoxical prediction that CO_2 -limitation within the symbiont population ultimately underpins the energetic disruption of host Ca^{2+} -ATPase, it is consistent that experimental addition of HCO_3^- (and its presumed extracellular dehydration to $\text{CO}_{2(\text{aq})}$) helps to temporarily forestall the deleterious impact of rising $p\text{CO}_2$ on coral calcification (Hertford et al., 2008; Marubini et al., 2008). Secondly, since limited availability of DIN may restrict the underpinning turnover and loss of zooxanthellae associated with elevated $p\text{CO}_2$ conditions, it is consistent that reduced seawater DIN is beneficial in limiting the impact of rising $p\text{CO}_2$ on coral calcification (Renegar and Riegl, 2005). Finally, for nutrient-replete experimental conditions that permit an increase in the CSD of zooxanthellae, it is consistent that the most detrimental impact of elevated $p\text{CO}_2$ (760 ppmv) on P:R and calcification occurs when temperature is also elevated (Reynaud et al., 2003). It can be spec-

ulated that this impact sequence recorded by Reynaud et al. (2003) would have been even more enhanced if the experiment had been carried out at irradiance levels higher than the adopted $380 \mu\text{mol photon m}^{-2} \text{s}^{-1}$.

An important question that requires consideration is the extent to which the coral host could possibly down-regulate its CCMs in response to rising external $\text{CO}_{2(\text{aq})}$, and thus maintain a stable symbiosis. That the host CCMs are indelibly linked to the biomineralisation process of skeletal growth (Fig. 3) necessitates that any such down-regulation would be recorded as a decrease in calcification rate – which in itself may be a limiting constraint, since the coral as a colony needs to constantly compete for space (and light) with other benthic organisms. Yet, a precedent example may exist whereby two Mediterranean coral species were able to maintain their algal symbiosis within an artificially high seawater CO_2 environment by completely ceasing calcification and returning to a soft-bodied form (Fine and Tchernov, 2007). An argument can be made however, that any down-regulation of the host CCMs could only be of nutritional benefit to the host if the zooxanthellae were nutrient (growth) limited. In the case where the zooxanthellae are not growth-limited, an increased permitted reliance on “free” (passive) $\text{CO}_{2(\text{aq})}$ opens the opportunity for the zooxanthellae to photosynthesize and replicate completely autonomous to the returned-photosynthate requirements of the host (i.e. the zooxanthellae effectively become host parasites). In the alternative case wherein the zooxanthellae are growth-limited, the host can maintain its receipt of photosynthate, whilst at the same time benefiting from a reduced energy investment into the ATP-dependent CCMs. A recent experiment carried out within the oligotrophic surface waters of the Red Sea may support such an argument. In this case the observed decline in coral calcification (and small reduction in zooxanthellae density) with increasing seawater $\text{CO}_{2(\text{aq})}$ concentrations was complemented by an increase in somatic tissue growth – potentially representative of surplus energy storage (Krief et al., 2010). Clearly, additional research is needed to identify the extent to which declines in the activity levels of host CCMs (and associated calcification) are host-directed or the negative consequence of autotrophic disruption – including the associated (conditional) importance of the prevailing environmental conditions (e.g. nutrient supply, temperature and irradiance regime).

3.3 Timescale and rates of *Symbiodinium* evolution

Molecular phylogenetic analyses indicate that *Symbiodinium* are genetically diverse: consisting of at least eight major divergent lineages (clade A-H), with each clade containing multiple subclade genotypes (reviewed by Baker, 2003). The genetically diverse zooxanthellae types differ in their phenotypic response (e.g. growth rate, photosynthetic yield) to external conditions, particularly light and temperature (Kinzie et al., 2001; Rowan, 2004). Significantly, the clocked

phylogenetic tree for *Symbiodinium* across the Cenozoic reveals that the major diversifications in genotypes occurred during periods of global cooling and falling $p\text{CO}_2$ (Fig. 8a; Pochon et al., 2006), with the most spectacular explosion of symbiont types occurring during the mid- to late-Miocene when $p\text{CO}_2$ consistently remained below 260 ppmv. Notably, this period also coincides with the post-Miocene explosion of scleractinian corals with branching morphologies and the first appearance in the fossil record of large benthic foraminifera (*Miliolida*, *Soritidae*) that host *Symbiodinium* (reviewed by Pochon and Pawlowski, 2006). Whilst an enhanced potential for allopatric differentiation within the expanding range of host habitat provides a likely evolutionary vehicle for *Symbiodinium* diversification (LaJeunesse, 2004), the proposed bleaching model identifies the permitted stability of the intracellular symbiosis below $p\text{CO}_2 = 260$ ppmv as an important pre-conditioning trigger for the enablement of the expanded host habitat (see next).

4 Geological evidence of symbiosis disruption beyond $p\text{CO}_2 = 260$ ppmv

If the outlined disruption to the cnidarian-*Symbiodinium* symbiosis around the $p\text{CO}_2 = 260$ ppmv threshold is physiologically significant, then its geological signature within ancient reef structures should be strong and consistent, especially in terms of the temporal (re)organisation of coral reef communities. Three important characteristics are predicted: (i) increased susceptibility to nutrient-driven disruption of the symbiosis when seawater $p\text{CO}_2 > 260$ ppmv, (ii) preferential selection for particular colony morphology types, with branching architectures favoured when seawater $p\text{CO}_2 < 260$ ppmv and massive growth forms favoured for $p\text{CO}_2 > 260$ ppmv, and (iii) selective constraints on the bathymetric zonation of reef structures, with mesophotic (deeper, lower-light) settings favoured when seawater $p\text{CO}_2 > 260$ ppmv and euphotic (shallower, near-full sunlight) settings favoured for $p\text{CO}_2 < 260$ ppmv.

4.1 Late Cenozoic turnover of Caribbean reefs

The late Cenozoic history of Caribbean coral reef ecosystem supports the reef community change predicted around the seawater $p\text{CO}_2 = 260$ ppmv threshold (Fig. 8b). About half the reef-building Caribbean corals died out during the latest Oligocene through early Miocene, about 24–16 Ma (Edinger and Risk, 1995). Prior to the late Oligocene event (i.e. $p\text{CO}_2 > 260$ ppmv) the community was dominated by massive and encrusting forms (Edinger and Risk, 1995). Zooxanthellate organisms were the primary victims of the Oligocene-Miocene extinction, with an enhanced upwelling supply of inorganic nutrients the proximal event trigger (Edinger and Risk, 1995). The subsequent recovery, across the Miocene to Pliocene transition ($p\text{CO}_2 < 260$ ppmv) was

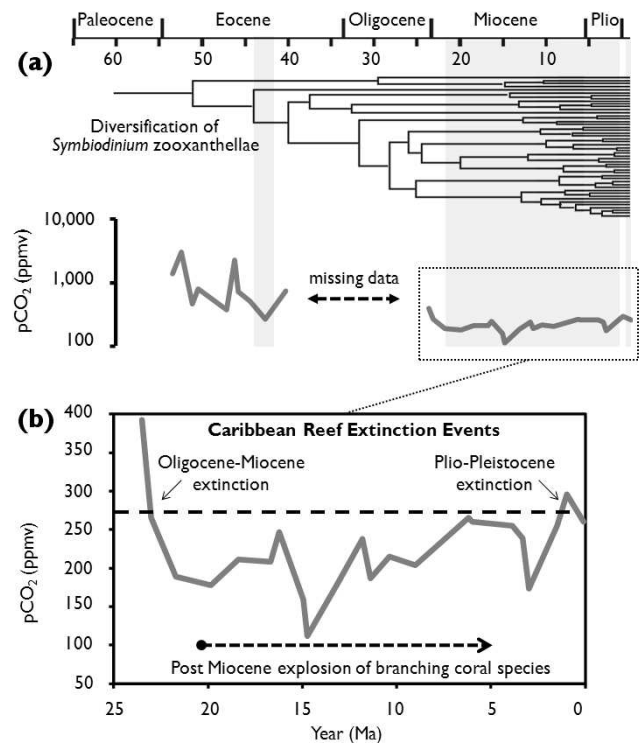


Fig. 8. (a) Chronogram of divergence timing of symbiotic dinoflagellate *Symbiodinium* established by molecular phylogeny (after Pochon et al., 2006). The mid-Miocene diversification of most extant lineages coincided with global cooling and a fall in $p\text{CO}_2$ below ~ 260 ppmv (nb: the $p\text{CO}_2$ reconstruction is based on the lower-bound (error considered) predictions of Pearson and Palmer, 2000). (b) Apparent synchronisation of late Cenozoic extinction and origination events on Caribbean coral reefs around the $p\text{CO}_2 = 260$ ppmv threshold.

characterised by high rates of speciation and a dramatic explosion of coral species with branching architectures (Johnson et al., 1995). This post-Miocene ascendance of large scale *Acropora* assemblages opened up new ecospace for the evolution of the myriad of creatures that now comprise our modern coral reefs. Evidence from the Mediterranean indicates that Miocene reef recovery proceeded through a mesophotic \rightarrow euphotic bathymetric zonation as seawater $p\text{CO}_2$ fell below 260 ppmv (Pomar and Hallock, 2007). Following the Miocene epoch (between 4–1 Ma), a peak of species origination preceded a significant extinction event ($\sim 50\%$ of reef-building corals) at the Pliocene-Pleistocene boundary, which culminated in a peak extinction rate from 2–1 Ma (Budd and Johnson, 1999; Budd, 2000). The extinction event corresponds with seawater $p\text{CO}_2 > 260$ ppmv, and consistent with the expected community-level restructuring, species with massive or platy shapes were more likely to survive than species with free-living or branching shapes (Johnson et al., 1995; Budd and Johnson, 1999).

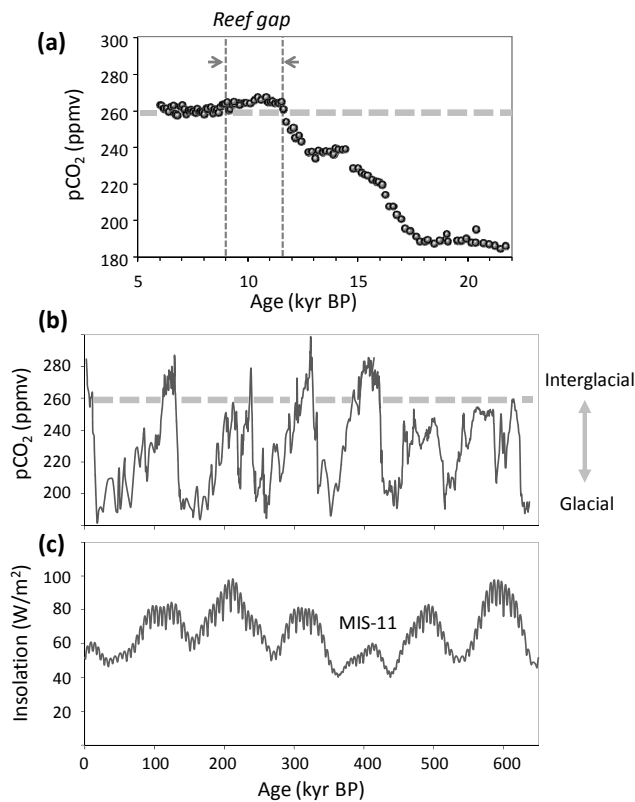


Fig. 9. (a) Deglacial rise in atmospheric CO_2 as recorded by ice core samples taken at Antarctica Dome C (Monnin et al., 2001). A notable “reef gap” in the geological record corresponds with the early Holocene exceedence of the 260 ppmv CO_2 threshold between 11.5 and 9 kyr BP (Montaggioni, 2000, 2005). (b) Extended records of atmospheric CO_2 for the last 650 kyr BP (Sigenthaler et al., 2005) highlight that the transition sequence from interglacial \rightarrow glacial conditions is repeatedly triggered $\sim 260\text{--}280$ ppmv. (c) The time evolution of the maximum amplitude of the seasonal cycle of 24-h mean irradiance at the equator (Berger et al., 2006) draws attention to the coherence with the ~ 100 kyr periodicity of glacial/interglacial climate cycles. Also evident, is the comparable (dampened) irradiance during the most recent glacial-interglacial sequence and MIS-11 (~ 400 kyr BP).

4.2 “Drowned” reefs at interglacial climate terminations

Paleoclimate $p\text{CO}_2$ reconstructions for the last glacial-interglacial transition (starting ~ 21 kyr BP) indicate an early Holocene exceedence of the 260 ppmv threshold between ~ 11.5 and 9 kyr BP (Fig. 9a; Monnin et al., 2001). This exceedence window corresponds with a notable “reef gap” in the geological record, wherein few reefs escaped demise (Montaggioni, 2000, 2005). Indeed, most reefs that existed just prior to 11.5 kyr BP are at present encountered as “drowned” relict features and terraces at depths of 40–70 m along the outer edges of most tropical continental shelves (reviewed by Montaggioni, 2000, 2005). Tentative explanation

for this global reef submergence event has previously centred on a proposed rapid rise in sea level associated with an ice-melt discharge ~ 11.5 kyr BP (Melt-water pulse 1B; Fairbanks, 1989), though the global extent and significance of this sea level rise is controversial, especially in terms of its exclusive role in halting reef growth (see e.g. Bard et al., 2010; Stanford et al., 2010). Part of the confusion in interpreting the eustatic sea level/reef accretion record may relate to the predicted (bleaching-induced) mortality response associated with exceeding the 260 ppmv $p\text{CO}_2$ threshold; permitted in part, by the co-occurrence of nutrient-replete conditions resulting from: (i) the enhanced upwelling supply of DIN into surface waters associated with the Melt-water pulse 1B event (Montaggioni, 2000, 2005, and references within), and/or (ii) the release of lowstand-stored terrestrial nutrients as the sea level rose over the continental margin and onto the shelf (Hallock and Schlager, 1986). For example, at the rare sites where continuous glacial-interglacial reef growth is recorded (e.g. Vanuatu; Cabioch et al., 2003), an abrupt rise in sea level ~ 11.5 kyr BP is inferred by the rapid change in the shallow-water community composition from a branching *Acropora*-dominated assemblage, to (an assumed deeper) massive *Porites*-dominated assemblage. Yet, this rapid community switch is equally predicted by the proposed differential selection against branching growth forms as seawater $p\text{CO}_2$ exceeded 260 ppmv.

The ocean alkalinity equilibrating mechanism of “carbonate compensation” (Broecker and Peng, 1987; Hodell et al., 2001) dictates that the geological signature of the low-latitude reef demise between 11.5 and 9 kyr BP is ultimately recorded in the deep-sea calcium carbonate (CaCO_3) preservation record and its associated link to atmospheric $p\text{CO}_2$. The temporal sequence for ocean basins linked to the transport of tropical waters can thus be understood as follows: (i) reef demise starting at 11.5 kyr BP triggers a transient increase in surface water alkalinity (i.e. increased $[\text{CO}_3^{2-}]$), as evidenced by a conspicuous increase in the productivity of calcifying plankton (e.g. coccolithophores; Flores et al., 2003). (ii) Shallow-to-deep ocean ventilation of this high alkalinity water mass with a mixing lag of ~ 2.5 kyr (Berger, 1982) acts to deepen the calcite lysocline around 7–9 kyr BP, as evidenced by a deep sea CaCO_3 preservation event (Broecker et al., 1993; Hodell et al., 2001; Marchitto et al., 2005; Klöcker and Henrich, 2006). (iii) The inverse relationship between the carbonate ion content of the deep-ocean and atmospheric $p\text{CO}_2$ (Broecker and Peng, 1987) links this lysocline deepening with the recorded draw-down in atmospheric $p\text{CO}_2$ between 7–9 kyr BP. It is thus consistent that major global cooling (e.g. the “8.2 kyr BP” cooling event; Alley et al., 1997) is centred around this reef-demise triggered $p\text{CO}_2$ drawdown sequence.

In this way, the enhanced susceptibility of the cnidarian-*Symbiodinium* symbiosis to irradiance-driven disruption at $p\text{CO}_2 > 260$ ppmv is forwarded here as a potential driver of interglacial \rightarrow glacial climate transitions, which for at

least the last 600 kyr have been repeatedly triggered ~ 260 – 280 ppmv (Fig. 9b; Sigenthaler et al., 2005). Verification of this suggestion requires sensitivity testing with a coupled atmosphere-ocean-sediment carbon cycle model. However, if true, then the dampened (Milankovitch-scale) equatorial insolation during the most recent glacial-interglacial period (Fig. 9c; Berger et al., 2006) has important (constraining) ramifications for the strength of the prescribed cooling sequence, and thus the likely duration of the present interglacial period. Firstly, because of the comparatively low insolation maximum, the predicted bleaching events beyond the 260 ppmv threshold are likely to have been less severe than they might otherwise be. Accordingly, the high alkalinity triggered deep-sea preservation sequence would be less significant than it might otherwise be; translating into a smaller drawdown in atmospheric $p\text{CO}_2$, and hence, a less influential cooling impact. Combining this lowered cooling impact with the concurrent dampened insolation (=lowered irradiance-driven symbiotic demand for CO_2) is suggested to provide the relatively unique opportunity whereby prolonged tropical reef growth can occur on the flooded continental shelf margin. Indeed, modelling identifies late Holocene coral reef buildup as a likely candidate for the observed ~ 20 ppmv rise in $p\text{CO}_2$ (and subsequent warming reversal) after the ~ 8 kyr BP cooling event (Ridgwell et al., 2003; Kleinen et al., 2010). By analogy with its comparable insolation dynamics, possibly the last time that such a warming reversal would have been permitted was during the interglacial centred on marine isotope stage (MIS) 11 (~ 400 kyr BP). Notably, MIS-11 is known for its extensive tropical-shelf reef growth, and extended (~ 30 kyr) interglacial period (Droxler et al., 1997; Droxler and Farrell, 2000).

The deep ocean CaCO_3 record provides persuasive evidence to support the unique (extended) period of shelf reef growth during both MIS-11 and the present interglacial. Again calling on the notion of steady state, enhanced CaCO_3 deposition on the shelves must ultimately be matched by enhanced dissolution of deep sea sediments. Notably, MIS-11 records the most significant deep-sea CaCO_3 dissolution for any of the late-Pleistocene glacial cycles, with a similar magnitude of change emerging from the present-day (corrosive) deep sea conditions (see e.g. Barker et al., 2006; Anderson et al., 2007).

4.3 The modern decline in coral diversity and abundance

The MIS-11 analogue indicates that shallow-water reef buildup (and its CaCO_3 -compensated $p\text{CO}_2$ increase) during the Holocene would have initiated a self-limiting feedback around pre-industrial $p\text{CO}_2 = 280$ ppmv; with the permitted 20 ppmv increase in seawater $p\text{CO}_2$ beyond the proposed autotrophic threshold (~ 260 ppmv) reconciled by low (Milankovitch-scale) equatorial insolation and improved shelf water quality in the later stages of the Holocene. Yet,

this permitted stasis of late Holocene reef growth has been recently disrupted by the precipitous (anthropogenic-driven) rise in seawater $p\text{CO}_2$ since the start of the industrial revolution (late 1700s), with its greatest impact on branching coral communities in nutrient-replete (i.e. coastal or upwelling) settings. Multiple studies confirm the extent and timing of the differential selection against symbiotic corals with branching architectures. For example, the drilling record recovered by Aronson et al. (2004) details that for at least 2000–3000 years prior to the last several decades, Belizean reefs were dominated by the staghorn coral *Acropora cervicornis*. The present day reefs in Belize however, have become dominated to a historically unprecedented extent, by the lettuce coral *Agaricia tenuifolia*; a coral whose ability to survive in turbid, nutrient-enriched habitats (Shyka and Sebens, 2000) suggests that it can readily switch to a heterotrophic mode of nutrition. The recent demise of branching corals after long-term periods of persistence and stability has also been replicated in Florida and the Bahamas (Greenstein et al., 1998), the Caribbean (Pandolfi and Jackson, 2006), and Panama (Aronson et al., 2004). Branching species have also been differentially selected against during recent bleaching episodes throughout the Indo-Pacific (Marshall and Baird, 2000; Loya et al., 2001). Interestingly, reports of thriving modern zooxanthellate coral communities in mesophotic depths in the Gulf of Mexico (e.g. Lang et al., 2001), at the same time Florida's shallow water reefs are in perilous decline (Greenstein et al., 1998), provide the basis for speculation that ongoing anthropogenically-driven global climate change and ocean acidification may drive zooxanthellae corals back into mesophotic depths (Bongaerts et al., 2010).

5 Concluding comments and prospects

New insights into the functioning of shallow-water cnidarian symbioses predict that the *realised* size of the algal symbiont population is in constant dispute between the partners (Wooldridge, 2009a, 2010). Moreover, the effectiveness of host mechanisms to limit (or reverse) the rapid proliferation potential of its algal partner appears linked to the prevailing envelope of environmental conditions. In particular, for modern corals the disrupting influence of warm, nutrient-replete seawater conditions has been noted (Wooldridge and Done, 2009; Wooldridge, 2009a, b). In this paper, the additional role of seawater $p\text{CO}_2$ has been explored, and the potential significance of the 260 ppmv threshold alluded. Specifically, for circumstances where the effectiveness of pre-mitotic controls on zooxanthalle proliferation rates is restricted (e.g. warm, nutrient-replete seawater conditions) it has been proposed that optimal (stable) functioning of cnidarian symbioses requires seawater $p\text{CO}_2 < 260$ ppmv, particularly for high irradiance (i.e. shallow-water) conditions. The corollary is that optimal functioning for $p\text{CO}_2 > 260$ ppmv is conditional on effective pre-mitotic control of

zooxanthalle proliferation rates, most readily achieved in nutrient-impooverished seawater.

The unifying capacity of this identified biological process/threshold to explain historical ocean extinction events (and linked atmospheric climate variability) has been suggested here to unveil a new level of determinism for the characteristic dynamics (and drivers) of the land-ocean-atmosphere carbon cycle of the Earth System. This new viewpoint draws attention to the primacy of low-latitude (tropical) insolation cycles, and its feedback interactions with shallow and deep-water CaCO_3 production/dissolution, for explaining the consistent upper (termination) $p\text{CO}_2$ threshold during the interglacial phase of Pleistocene climate cycles. Moreover, the coherence of Milankovitch-scale variations in equatorial insolation with the ~ 100 kyr periodicity of glacial-interglacial climate cycles (Fig. 9c; Berger et al., 2006; Ashkenazy and Gildor, 2008) also alludes to the fundamental importance of a tropical-driver for the opposing glacial \rightarrow interglacial climate transition. Given the contextual evidence provided here, there appears little reason to suggest that temperature/irradiance feedbacks upon the rates of shallow and deep-water CaCO_3 production/dissolution (via its compensated impact upon atmospheric $p\text{CO}_2$) will not also play a prominent role in driving the glacial termination sequence. Future testing with a coupled atmosphere-ocean-sediment carbon cycle model offers considerable scope for verifying the proposed relevance of shallow water CaCO_3 dynamics to the termination sequence of both the glacial and interglacial phases of Pleistocene climate cycles.

Significantly, the new construct for the causes and process of coral bleaching has ominous implications for the viability of shallow-water tropical reef ecosystems during the present human-dominated (“Anthropocene”) era of the Earth System. Indeed, it suggests that an extinction event may already be underway that has the potential to rival the Pliocene-Pleistocene and Oligocene-Miocene events. It follows that global efforts are needed as a matter of urgency to halt and reverse the present-day trajectory of rapidly rising $p\text{CO}_2$. The complementary benefits offered by local efforts to limit coastal eutrophication (see e.g. Wooldridge et al., 2012) should also not be underestimated. Future testing and refinement of the ideas presented within this paper offers considerable hope for developing further insights into tackling the climate-induced demise of cnidarian-*Symbiodinium* symbioses and the reefs they construct.

Edited by: U. Riebesell

References

- Al-Horani, F. A., Al-Moghrabi, S. M., and De Beer, D.: Microsensor study of photosynthesis and calcification in the scleractinian coral, *Galaxea fascicularis*: active internal carbon cycle, J. Exp. Mar. Biol. Ecol., 288, 1–15, 2003a.
- Al-Horani, F. A., Al-Moghrabi, S. M., and De Beer, D.: The mechanism of calcification and its relation to photosynthesis and respiration in the scleractinian coral, *Galaxea fascicularis*, Mar. Biol., 142, 419–426, 2003b.
- Alley, R. B., Mayewski, P. A., Sowers, T., Stuiver, M., Taylor, K. C., and Clark, P. U.: Holocene climatic instability: a prominent, widespread event 8200 yr ago, Geol., 25, 483–486, 1997.
- Anderson, R. F., Fleisher, M. Q., Lao, Y., and Winckler, G.: Modern CaCO_3 preservation in equatorial Pacific sediments in the context of late-Pleistocene glacial cycles, Mar. Chem., 111, 30–46, 2007.
- Anthony, K. R. N., Kline, D. I., Diaz-Pulido, G., Dove, S., and Hoegh-Guldberg, O.: Ocean acidification causes bleaching and productivity loss in coral reef builders, PNAS, 105, 17442–17446, 2008.
- Anthony, K. R. N., Hoogenboom, M. O., Grotoli, A., Middlebrook, R., and Maynard, J.: Energetics approach to predicting mortality risk from environmental stress: a case study of coral bleaching, Funct. Ecol., 23, 539–550, 2009.
- Aronson, R. B., Macintyre, I. G., Wapnick, C. M., and O’Neill, M. W.: Phase shifts, alternative states, and unprecedented convergence of two reef systems, Ecology, 85, 1876–1891, 2004.
- Ashkenazy, Y. and Gildor, H.: Timing and significance of maximum and minimum equatorial insolation, Paleoceanography, 23, PA1206, doi:10.1029/2007PA001436, 2008.
- Baker, A. C.: Flexibility and specificity in coral-algal symbiosis: diversity, ecology, and biogeography of *Symbiodinium*, Annu. Rev. Ecol. Syst., 34, 661–689, 2003.
- Bard, E., Hamelin, B., and Delanghe-Sabatier, D.: Deglacial Meltwater Pulse 1B and the Younger Dryas sea levels revisited with boreholes at Tahiti, Science, 327, 1235–1237, 2010.
- Barker, S., Archer, D., Booth, L., Elderfield, H., Henderiks, J., and Rickaby, R. E. M.: Globally increased pelagic carbonate production during the Mid-Brunhes dissolution interval and the CO_2 paradox of MIS 11, Quaternary Sci. Rev., 25, 3278–3293, 2006.
- Berger, W. H.: Deglacial CO_2 buildup: constraints on the coral-reef model, Palaeogeogr. Palaeoclimatol. Palaeoecol., 40, 235–253, 1982.
- Berger, A., Loutre, M. F., and Mélice, J. L.: Equatorial insolation: from precession harmonics to eccentricity frequencies, Clim. Past, 2, 131–136, doi:10.5194/cp-2-131-2006, 2006.
- Berkelmans, R. and Willis, B. L.: Seasonal and local spatial patterns in the upper thermal limits of corals on the inshore Central Great Barrier Reef, Coral Reefs, 18, 219–228, 1999.
- Bhagooli, R. and Hidaka, M.: Physiological responses of the coral *Galaxea fascicularis* and its algal symbiont to elevated temperatures, Galaxea, 4, 33–42, 2002.
- Bongaerts, P., Ridgway, T., Sampayo, E. M., and Hoegh-Guldberg, O.: Assessing the ‘deep reef refugia’ hypothesis: focus on Caribbean reefs, Coral Reefs, 29, 309–327, 2010.
- Broecker, W. S. and Peng, T. H.: The role of CaCO_3 compensation in the glacial to interglacial CO_2 change, Paleoceanography, 13, 352–364, 1987.
- Broecker, W. S., Lao, Y., Klas, M., Clark, E., Bonani, G., Ivy, S., and Chen, C.: A search for an early Holocene CaCO_3 preservation event, Paleoceanography, 8, 333–339, 1993.

- Budd, A. F.: Diversity and extinction in the Cenozoic history of Caribbean reefs, *Coral Reefs*, 19, 25–35, 2000.
- Budd, A. F. and Johnson, K. G.: Origination preceding extinction during late Cenozoic turnover of Caribbean reefs, *Paleobiology*, 25, 188–200, 1999.
- Cabioch, G., Banks-Cutler, K. A., Beck, W. J., Burr, G. S., Correge, T., Edwards, R. L., and Taylor, F. W.: Continuous reef growth during the last 23 cal kyr BP in a tectonically active zone (Vanuatu, South-West Pacific), *Quaternary Sci. Rev.*, 22, 1771–1786, 2003.
- Carpenter, L. W. and Patterson, M. R.: Water flow influences the distribution of photosynthetic efficiency within colonies of the scleractinian coral *Montastrea annularis* (Ellis and Solander, 1786); implications for coral bleaching, *J. Exp. Mar. Biol. Ecol.*, 351, 10–26, 2007.
- Chauvin, A., Denis, V., and Cuet, P.: Is the response of coral calcification to seawater acidification related to nutrient loading?, *Coral Reefs*, 30, 911–923, doi:10.1007/s00338-011-0786-7, 2011.
- Cohen, A. L. and Holcomb, M.: Why corals care about ocean acidification: uncovering the mechanism, *Oceanography*, 22, 118–127, 2009.
- Coles, S. L. and Jokiel, P. L.: Effects of temperature on photosynthesis and respiration in hermatypic corals, *Mar. Biol.*, 43, 209–216, 1977.
- D’Croz, L., Mate, J. L., and Oke, J. E.: Responses to elevated sea water temperature and uv radiation in the coral *Porites lobata* from upwelling and non-upwelling environments on the pacific coast of Panama, *B. Mar. Sci.*, 69, 203–214, 2001.
- Denny, M. W.: *Biology and the mechanics of the wave-swept environment*, Princeton University Press, Princeton, NJ, 1988.
- Droxler, A. W. and Farrell, J. W.: Marine Isotope Stage 11 (MIS 11): new insights for a warm future, *Global Planet. Change*, 24, 1–5, 2000.
- Droxler, A. W., Ferro, E. C., Mucciarone, D. A., and Haddad, G. A.: The marine carbonate system during oxygen isotope stage 11 (423–362 ka): a case of basin-to-shelf and/or basin-to-basin carbonate fractionation?, *Eos (Trans. Am. Geophys. Union)*, 78, S179, 1997.
- Dubinsky, Z. and Berman-Frank, I.: Uncoupling primary production from population growth in photosynthesizing organisms in aquatic ecosystems, *Aquat. Sci.*, 63, 4–17, 2001.
- Dubinsky, Z. and Jokiel, P. L.: Ratio of energy and nutrient fluxes regulates symbiosis between zooxanthellae and corals, *Pac. Sci.*, 48, 313–324, 1994.
- Edinger, E. N. and Risk, M. J.: Oligocene-Miocene extinction and geographic restriction of Caribbean corals: roles of turbidity, temperature, and nutrients, *Palaos*, 9, 576–598, 1995.
- Fairbanks, R. G.: A 17,000-year glacio-eustatic sea level record: Influence of glacial melting rates on the Younger Dryas event and deep-ocean circulation, *Nature*, 342, 637–642, 1989.
- Fang, L. S., Chen, Y. W., and Chen, C. S.: Why does the white tip of stony coral grow so fast without zooxanthellae?, *Mar. Biol.*, 103, 359–363, 1989.
- Ferrier-Pagès, C., Schoelzke, V., Jaubert, J., Muscatine, L., and Hoegh-Guldberg, O.: Response of a scleractinian coral, *Stylophora pistillata*, to iron and nitrate enrichment, *J. Exp. Mar. Biol. Ecol.*, 259, 249–261, 2001.
- Fine, M. and Tchernov, D.: Scleractinian coral species survive and recover from decalcification, *Science*, 315, 1811, 2007.
- Fitt, W. K., McFarland, F. K., Warner, M. E., and Chilcoat, G. C.: Seasonal patterns of tissue biomass and densities of symbiotic dinoflagellates in reef corals and relation to coral bleaching, *Limnol. Oceanogr.*, 45, 677–685, 2000.
- Flores, J. A., Marino, M., Sierro, F. J., Hodell, D. A., and Charles, C. D.: Calcareous plankton dissolution pattern and coccolithophore assemblages during the last 600 kyr at ODP Site 1089 (Cape Basin, South Atlantic): paleoceanographic implications, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 196, 409–426, 2003.
- Furla, P., Allemand, D., and Orsenigo, M. N.: Involvement of H^+ -ATPase and carbonic anhydrase in inorganic carbon uptake for endosymbiont photosynthesis, *Am. J. Physiol.*, 278, 870–881, 2000.
- Genin, A., Lazar, B., and Brenner, S.: Vertical mixing and coral death in the Red-Sea following the eruption of mount-Pinatubo, *Nature*, 377, 507–510, 1995.
- Gleason, D. F. and Wellington, G. M.: Ultraviolet radiation and coral bleaching, *Nature*, 365, 836–838, 1993.
- Gordillo, F. J. L., Jiménez, C., Figueroa, F. L., and Niell, F. X.: Influence of elevated CO_2 and nitrogen supply on the carbon assimilation performance and cell composition of the unicellular alga *Dunaliella viridis*, *Physiol. Plant.*, 119, 513–518, 2003.
- Greenstein, B. J., Curran, A., and Pandolfi, J. M.: Shifting ecological baselines and the demise of *Acropora cervicornis* in the western North Atlantic and Caribbean Province: a Pleistocene perspective, *Coral Reefs*, 17, 249–261, 1998.
- Grimsditch, G., Mwaura, J., Kilonzo, J., Amiyo, N., and Obura, D.: High zooxanthellae densities and turnover correlate with low bleaching tolerance in Kenyan corals, in: *Ten Years After Bleaching – Facing the Consequences of Climate Change in the Indian Ocean*, CORDIO Status Report 2008, CORDIO, Mombasa Kenya, 235–236, 2008.
- Hallock, P. and Schlager, W.: Nutrient excess and the demise of coral reefs and carbonate platforms, *Palaos*, 1, 389–398, 1986.
- Helmuth, B. S. T., Sebens, K. P., and Daniel, T. L.: Morphological variation in coral aggregations: branch spacing and mass flux to coral tissues, *J. Exp. Mar. Biol. Ecol.*, 209, 233–259, 1997.
- Hertford, L., Thake, B., and Taubner, I.: Bicarbonate stimulation of calcification and photosynthesis in two hermatypic corals, *J. Phycol.*, 44, 91–98, 2008.
- Hodell, D. A., Charles, C. D., and Sierro, F. J.: Late Pleistocene evolution of the ocean’s carbonate system, *Earth Planet. Sci. Lett.*, 192, 109–124, 2001.
- Hoegh-Guldberg, O. and Smith, G. J.: The effect of sudden changes in temperature, light and salinity on the population density and export of zooxanthellae from the reef corals *Stylophora pistillata* Esper and *Seriatopora hystrix* Dana, *J. Exp. Mar. Biol. Ecol.*, 129, 279–303, 1989.
- Hoegh-Guldberg, O., Muscatine, L., Goiran, C., Siggaard, D., and Marion, G.: Nutrient-induced perturbations to $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in symbiotic dinoflagellates and their hosts, *Mar. Ecol. Prog. Ser.*, 280, 105–114, 2004.
- Hoogenboom, M., Beraud, E., and Ferrier-Pagès, C.: Relationship between symbiont density and photosynthetic carbon acquisition in the temperate coral *Cladocora caespitosa*, *Coral Reefs*, 29, 21–29, 2010.
- Johnson, K. G., Budd, A. F., and Stemann, T. A.: Extinction selectivity and ecology of Neogene Caribbean corals, *Paleobiology*, 21, 52–73, 1995.

- Jones, R. J. and Yellowlees, D.: Regulation and control of intracellular algae (= zooxanthellae) in hard corals, *Philos. T. Roy. Soc. B*, 352, 457–468, 1997.
- Kawahata, H., Suzuki, A., and Goto, K.: Coral reef ecosystems as a source of atmospheric CO_2 : evidence from $p\text{CO}_2$ measurements of surface waters, *Coral Reefs*, 16, 261–266, 1997.
- Kinzie, R. A., Takayama, M., Santos, S. R., and Coffroth, M. A.: The adaptive bleaching hypothesis: experimental tests of critical assumptions, *Biol. Bull.*, 200, 51–58, 2001.
- Kleinen, T., Brovkin, V., von Bloh, W., Archer, D., and Munhoven, G.: Holocene carbon cycle dynamics, *Geophys. Res. Lett.*, 37, L02705, doi:10.1029/2009GL041391, 2010.
- Kleypas, J. A. and Langdon, C.: Coral reefs and changing seawater chemistry, in: *Coral Reefs and Climate Change: Science and Management*, AGU Monograph Series, Coastal and Estuarine Studies, American Geophysical Union, Washington D.C., 61, 73–110, 2006.
- Kleypas, J. A., Buddemeier, R. W., Archer, D., Gattuso, J. P., Langdon, C., and Opdyke, B. N.: Geochemical consequences of increased atmospheric carbon dioxide on coral reefs, *Science*, 284, 118–120, 1999.
- Klöcker, R. and Henrich, R.: Recent and Late Quaternary pteropod preservation on the Pakistan shelf and continental slope, *Mar. Geol.*, 231, 103–111, 2006.
- Krief, S., Hendy, E. J., Fine, M., Yam, R., Meibom, A., Foster, G. L., and Shemesh, A.: Physiological and isotopic responses of scleractinian corals to ocean acidification, *Geochim. Cosmochim. Acta*, 74, 4988–5001, 2010.
- LaJeunesse, T. C.: ‘Species’ radiations of symbiotic dinoflagellates in the Atlantic and Indo-Pacific since the Miocene-Pliocene transition, *Mol. Biol. Evol.*, 22, 570–581, 2004.
- Lang, J. C., Deslarzes, K. J. P., and Schmahl, G. P.: The Flower Garden Banks: Remarkable reefs in the NW Gulf of Mexico, *Coral Reefs*, 20, 126, 2001.
- Loya, Y., Sakai, K., Yamazato, K., Nakano, Y., Sambali, H., and van Woesik, R.: Coral bleaching: the winners and the losers, *Ecol. Letters*, 4, 122–131, 2001.
- Marchitto, T. M., Lynch-Stieglitz, J., and Hemming, S. R.: Deep Pacific CaCO_3 compensation and glacial-interglacial atmospheric CO_2 , *Earth Planet. Sci. Lett.*, 231, 317–336, 2005.
- Marshall, P. A. and Baird, A. H.: Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa, *Coral Reefs*, 19, 155–163, 2000.
- Marubini, F., Ferrier-Pagès, C., Furla, P., and Allemand, D.: Coral calcification responds to seawater acidification: a working hypothesis, *Coral Reefs*, 27, 491–499, 2008.
- Mass, T. and Genin, A.: Environmental versus intrinsic determination of colony symmetry in the coral *Pocillopora verrucosa*, *Mar. Ecol. Prog. Ser.*, 369, 131–137, 2008.
- McClanahan, T. R., Maina, J., Moothien-Pillay, R., and Baker, A. C.: Effects of geography, taxa, water flow, and temperature variation on coral bleaching intensity in Mauritius, *Mar. Ecol. Prog. Ser.*, 298, 131–142, 2005.
- McConnaughey, T. A. and Whelan, J. F.: Calcification generates protons for nutrient and bicarbonate uptake, *Earth Sci. Rev.*, 42, 95–117, 1997.
- McGuire, M. P. and Szmant, A. M.: Time course of physiological responses to NH_4 enrichment by a coral-zooxanthellae symbiosis, in: *Proceedings of the 8th Coral Reef Symposium*, Smithsonian Tropical Research Institute, 24–29 June, Panama City, Panama, 909–914, 1997.
- Monnin, E., Indermühle, A., Dällenbach, A., Flückiger, J., Stauffer, B., Stocker, T. F., Raynaud, D., and Barnola, J.-M.: Atmospheric CO_2 concentrations over the last glacial termination, *Science*, 291, 112–114, 2001.
- Montaggioni, L. F.: Postglacial reef growth, *C.R. Acad. Sci. II A*, 331, 319–330, 2000.
- Montaggioni, L. F.: History of Indo-Pacific coral reef systems since the last glaciation: Development patterns and controlling factors, *Earth Sci. Rev.*, 71, 1–75, 2005.
- Muller-Parker, G. and Davy, S. K.: Temperate and tropical algal-sea anemone symbioses, *Invertebr. Biol.*, 120, 104–123, 2001.
- Muscatine, L., Porter, J. W., and Kaplan, I. R.: Resource partitioning by reef corals as determined from stable isotope composition: I. $\delta^{13}\text{C}$ of zooxanthellae and animal tissue vs. Depth, *Mar. Biol.*, 100, 185–193, 1989.
- Muscatine, L., Ferrier-Pages, C., Blackburn, A., Gates, R. D., Baghdasarian, G., and Allemand, D.: Cell-specific density of symbiotic dinoflagellates in tropical anthozoans, *Coral Reefs*, 17, 329–337, 1998.
- Najjar, R. G.: Marine Biogeochemistry, in: *Climate System Modeling*, Cambridge University Press, Cambridge, England, 241–280, 1992.
- Naim, O.: Seasonal responses of a fringing reef community to eutrophication (Reunion Island, Western Indian Ocean), *Mar. Ecol. Prog. Ser.*, 99, 137–151, 1993.
- Nakamura, T., Yamasaki, H., and van Woesik, R.: Water flow facilitates recovery from bleaching in the coral *Stylophora pistillata*, *Mar. Ecol. Prog. Ser.*, 256, 287–291, 2003.
- Nakamura, T., van Woesik, R., and Yamasaki, H.: Photoinhibition of photosynthesis is reduced by water flow in the reef-building coral *Acropora digitifera*, *Mar. Ecol. Prog. Ser.*, 301, 109–118, 2005.
- Okamoto, M., Nojima, S., Furushima, Y., and Nojima, H.: Evaluation of coral bleaching condition *in situ* using an underwater pulse amplitude modulated fluorometer, *Fisheries Sci.*, 71, 847–854, 2005.
- Oliver, J. K.: Intra-colony variation in the growth of *Acropora formosa*: extension rates and skeletal structure of white (zooxanthellae-free) and brown-tipped branches, *Coral Reefs*, 3, 139–147, 1984.
- Pandolfi, J. M. and Jackson, J. B. C.: Ecological persistence interrupted in Caribbean coral reefs, *Ecol. Letters*, 9, 818–826, 2006.
- Patterson, M. R., Sebens, K. P., and Olson, R. R.: In situ measurements of flow effects on primary production and dark respiration in reef corals, *Limnol. Oceanogr.*, 36, 936–948, 1991.
- Pearson, P. N. and Palmer, M. R.: Atmospheric carbon dioxide concentrations over the past 60 million years, *Nature*, 406, 695–699, 2000.
- Pecheux, M.: CO_2 increase, a direct cause of coral reef mass bleaching?, *Mar. Life*, 12, 63–68, 2002.
- Pomar, L. and Hallock, P.: Changes in coral-reef structure through the Miocene in the Mediterranean province: Adaptive versus environmental influence, *Geology*, 35, 899–902, 2007.
- Pochon, X. and Pawlowski, J.: Evolution of the soritids-*Symbiodinium* symbiosis, *Symbiosis*, 42, 77–88, 2006.
- Pochon, X., Montoya-Burgos, J. I., Stadelmann, B., and Pawlowski, J.: Molecular phylogeny, evolutionary rates, and divergence tim-

- ing of the symbiotic dinoflagellate genus *Symbiodinium*, Mol. Phylogenet. Evol., 38, 20–30, 2006.
- Porter, J. W., Fitt, W. K., Spero, H. J., Rogers, C. S., and White, M. W.: Bleaching in reef corals: physiological and stable isotopic responses, PNAS, 86, 9342–9346, 1989.
- Ravindran, J. and Raghukumar, C.: Pink-line syndrome, a physiological crisis in the scleractinian coral *Porites lutea*, Mar. Biol., 149, 347–356, 2006.
- Renegar, D. A. and Riegl, B. M.: Effect of nutrient enrichment and elevated CO_2 partial pressure on growth rate of Atlantic scleractinian coral *Acropora cervicornis*, Mar. Ecol. Prog. Ser., 293, 69–76, 2005.
- Reynaud, S., Leclercq, N., Romaine-lioud, S., Ferrier-pagés, C., Jaubert, J., and Gattuso, J. P.: Interacting effects of CO_2 partial pressure and temperature on photosynthesis and calcification in a scleractinian coral, Global Change Biol., 9, 1660–1668, 2003.
- Ridgwell, A. J., Watson, A. J., Maslin, M. A., and Kaplan, J. O.: Implications of coral buildup for the controls on atmospheric CO_2 since the last Glacial Maximum, Paleoceanography, 18, 1083, doi:10.1029/2003PA000893, 2003.
- Rodolfo-Metalpa, R., Martin, S., Ferrier-Pagès, C., and Gattuso, J.-P.: Response of the temperate coral *Cladocora caespitosa* to mid- and long-term exposure to $p\text{CO}_2$ and temperature levels projected for the year 2100 AD, Biogeosciences, 7, 289–300, doi:10.5194/bg-7-289-2010, 2010.
- Rowan, R.: Coral bleaching: thermal adaptation in reef coral symbionts, Nature, 430, 742, 2004.
- Sachs, J. L. and Wilcox, T. P.: A shift to parasitism in the jellyfish symbiont *Symbiodinium microadriaticum*, Proc. Roy. Soc. Lon. B Bio., 273, 425–429, 2006.
- Shenkar, N., Fine, M., and Loya, Y.: Size matters: bleaching dynamics of the coral *Oculina Patagonica*, Mar. Ecol. Prog. Ser., 94, 181–188, 2005.
- Shyka, T. A. and Sebens, K. P.: Community structure, water column nutrients, and water flow in two Pelican Cays ponds, Belize, Atoll Res. Bull., 471, 105–121, 2000.
- Sigenthaler, U., Stocker, T. F., Monnin, E., Lüthi, D., Schwander, J., Stauffer, B., Raynaud, D., Barnola, J. M., Fischer, H., Masson-Delmotte, V., and Jouzel, J.: Stable carbon cycle-climate relationship during the late Pleistocene, Science, 310, 1313–1317, 2005.
- Stanford, J. D., Hemingway, R., Rohling, E. J., Challenor, P. G., Medina-Elizalde, M., and Lester, A. J.: Sea-level probability for the last deglaciation: A statistical analysis of far-field records, Global Planet. Change, 79, 193–203, doi:10.1016/j.gloplacha.2010.11.002, 2010.
- Stanley, G. D.: Photosymbiosis and the evolution of modern coral reefs, Science, 312, 857–858, 2006.
- Stimson, J.: The annual cycle of density of zooxanthellae in the tissues of field and laboratory-held *Pocillopora damicornis* (Linnaeus), J. Exp. Mar. Biol. Ecol., 214, 35–48, 1997.
- Stimson, J. and Kinzie, R. A.: The temporal pattern and rate of release of zooxanthellae from the reef coral *Pocillopora damicornis* (Linnaeus) under nitrogen-enrichment and control conditions, J. Exp. Mar. Biol. Ecol., 153, 63–74, 1991.
- Strychar, K. B., Coates, M., and Sammarco, P. W.: Loss of *Symbiodinium* from bleached Australian scleractinian corals (*Acropora hyacinthus*, *Favites complanata* and *Porites solida*), Mar. Freshwater Res., 55, 135–144, 2004.
- Tomczak, M. and Godfrey, M. (Eds.): Regional Oceanography: An Introduction, Pergamon, London, 1994.
- Trench, R. K.: Microalgal-invertebrate symbioses: a review, Endocyt Cell Res., 9, 135–175, 1993.
- Verde, A. E. and McCloskey, L. R.: 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, 1996.
- Veron, J. E. N.: Corals in space and time: the biogeography and evolution of the scleractinians, Cornell University Press, Ithaca, New York, 1995.
- Wagner, D. E., Kramer, P., and van Woessik, R.: Species composition, habitat, and water quality influence coral bleaching in south-eastern Florida, Mar. Ecol. Prog. Ser., 408, 65–78, 2010.
- Wolf-Gladrow, D. A., Riebesell, U., Burkhardt, S., and Bijma, J.: Direct effects of CO_2 concentrations on growth and isotopic composition of marine plankton, Tellus, 51B, 461–476, 1999.
- Wooldridge, S. A.: A new conceptual model for the warm-water breakdown of the coral-algae endosymbiosis, Mar. Freshw. Res., 60, 483–496, 2009a.
- Wooldridge, S. A.: Water quality and coral bleaching thresholds: Formalising the linkage for the inshore reefs of the Great Barrier Reef, Australia, Mar. Poll. Bull., 58, 745–751, 2009b.
- Wooldridge, S. A.: Is the coral-algae endosymbiosis really ‘mutually-beneficial’ for the partners?, Bioessays, 32, 615–625, 2010.
- Wooldridge, S. A. and Done, T. J.: Improved water quality can ameliorate effects of climate change on corals, Ecol. Appl., 19, 1492–1499, 2009.
- Wooldridge, S. A., Done, T. J., Thomas, C., Gordon, I. I., Marshall, P. A., and Jones, R. N.: Safeguarding coastal coral communities on the central Great Barrier Reef (Australia) against climate change: realizable local and global actions, Clim. Change, 112, 945–961, doi:10.1007/s10584-011-0229-z, 2012.
- Yamashita, H., Suzuki, G., and Hayashibara, T.: Do corals select zooxanthellae by alternative discharge?, Mar. Biol., 158, 87–100, 2011.
- Yellowlees, D., Rees, T. A., and Leggat, W.: Metabolic interactions between algal symbionts and invertebrate hosts, Plant Cell Environ., 31, 679–694, 2008.