

Reef development and resilience to acute (El Niño warming) and chronic (high-CO₂) disturbances in the eastern tropical Pacific: a real-world climate change model

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Abstract It has been recently recognized that eastern tropical Pacific (ETP) coral reefs exist under naturally-occurring high-CO₂, low carbonate saturation (Ω) conditions that encompass the range of expected changes for the entire tropical surface ocean with a doubling and tripling of atmospheric CO₂. Holocene reef development positively and linearly tracks Ω in the ETP; illustrating the real-world importance of this variable on reef building. Galápagos reef communities have been subject to the most extreme thermal anomalies associated with the El Niño-Southern Oscillation (ENSO) and also experience the lowest Ω levels in the ETP. Reef resilience has been so poor in Galápagos that reef structures were completely bioeroded in < 10 years after the 1982-83 ENSO. The closure of the Panamanian isthmus 3-3.5 million years ago created the present-day oceanographic conditions responsible for ENSO-related warming events and the upwelling of high-CO₂ waters throughout the ETP. These combined acute (ENSO) and chronic (high-CO₂) disturbances may help explain why coral reefs are scant and many genera of corals went extinct in the ETP during the late Cenozoic; thus providing a real-world example of the combined thermal and chemical ramifications of climate change on coral reef structure, function and resilience to disturbance over geologic time.

Keywords Ocean acidification, Eastern tropical Pacific, Climate change, Reef development

Introduction

Coral reefs flourish in the tropics where temperatures are warm year-round (> 18°C), illumination is high/turbidity is low, and seawater is supersaturated with respect to calcium carbonate (CaCO₃) (Kleypas et al. 1999a). Considerable environmental variability has been recognized as detrimental to coral reef development since Charles Darwin's (1842) original treatise on the subject. The relative importance of the specific environmental variables eliciting this distributional hypothesis is less obvious. Elevated nutrients have been hypothesized to be particularly deleterious to coral reef development based upon the assumptions that nutrients stimulate water-column productivity and turbidity, thus limiting the light required by the photosynthetic endosymbionts of reef corals (Hallock 1988) (Fig. 1). Increased levels of nutrients and productivity are thought to favor the proliferation of fleshy benthic macroalgae (autotrophs) and heterotrophic communities (e.g. filter-feeding bioeroding organisms), respectively, at the expense of "mixotrophic" community assemblages like that of modern-day Scleractinian coral reefs (Hallock and Schlager 1986) (Fig. 1).

Also, Hallock and Schlager (1986) suggested that high concentrations of phosphate inhibit coral calcification given its potential to act as a poison to crystal formation (Simkiss 1964).

However, nearly all the evidence supporting this hypothesis is qualitative (e.g. Hallock and Schlager 1986; Hallock 1988) or high nutrient exposure experiments only elicit significant results on coral calcification at concentrations that would rarely, if ever occur in nature (Kinsey and Davies 1979; Ferrier-Pagès et al. 2000). Coral reefs do, in fact, persist under wide ranges of nutrients and turbidity (Smith and Jokiel 1978; Perry et al. 2008) and even reef areas thought to be oligotrophic experience variable and sometimes high levels of dissolved nutrients due to natural physical forcing mechanisms (Leichter et al. 2003). Several recent review papers have pointed out the tenuous links between nutrients, algal competition and coral reef decline (McCook et al. 2001; Szmant 2002). As Tomascik and Sander (1985) suggested, it is likely that nutrients themselves do not elicit the most negative effects *per se*, but rather the increase in water-column productivity, turbidity and accompanying decline in light levels

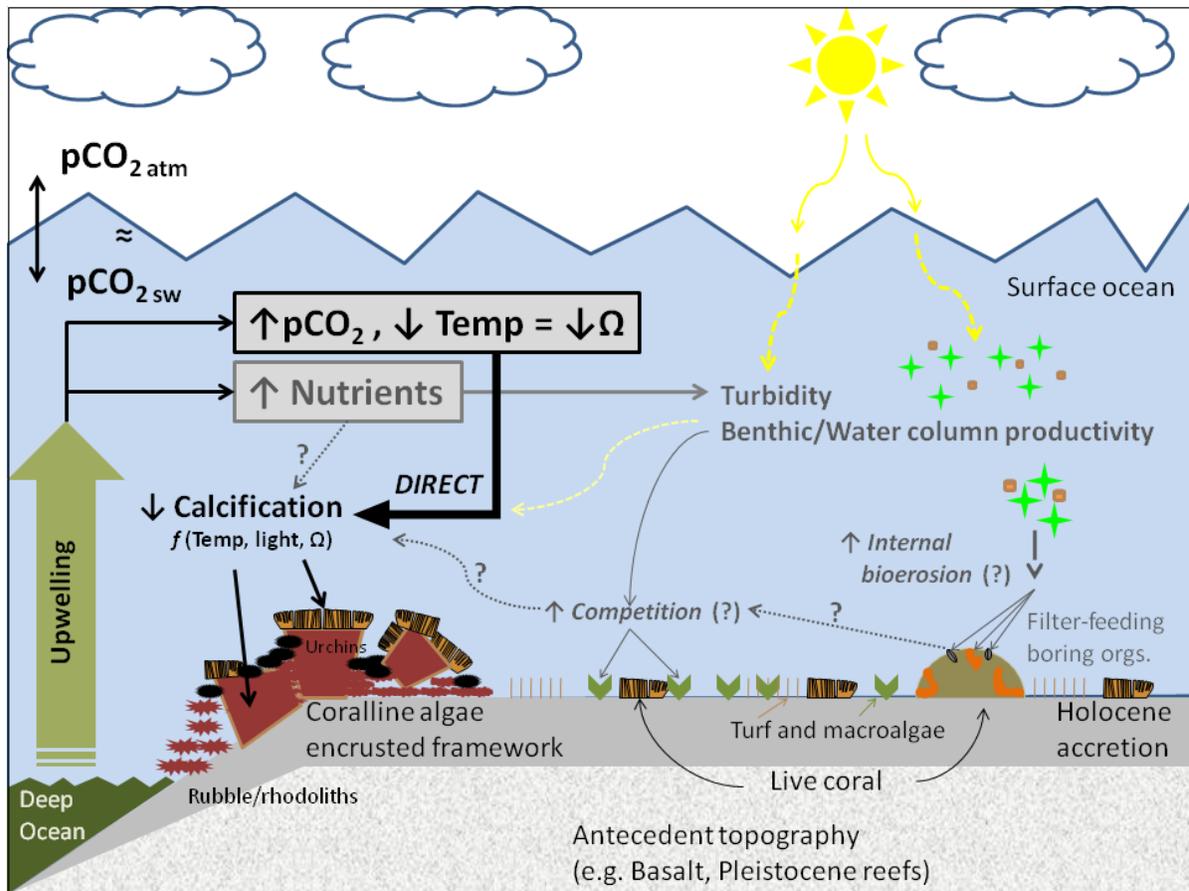


Fig. 1. Simplified model illustrating direct effects of high-pCO₂, low-Ω seawater on reef-building in an upwelling environment compared to primarily indirect effects of elevated nutrients (Smith and Buddemeier 1992).

that are associated with nutrient inputs (natural and anthropogenic) are most deleterious for reef corals.

Upwelling and reef development in the eastern Pacific

Upwelling areas experience highly heterogeneous environmental conditions that experience not only wide ranges in temperature, nutrients and turbidity, but recently it has been recognized that upwelled waters have a high partial pressure of carbon dioxide (high-pCO₂) (Takahashi et al. 1997). This high-pCO₂ effectively depresses the saturation state of CaCO₃ ($\Omega = [\text{Ca}^{2+}][\text{CO}_3^{2-}]/K'_{\text{sp}}$, where K'_{sp} is the solubility product of a carbonate mineral such as aragonite or calcite), which is a function of both CO₂ and temperature. Indeed, surface waters in many parts of the eastern tropical Pacific (ETP) have lower pH, lower Ω , and higher pCO₂ values relative to the rest of the tropics (Manzello et al. 2008). Given that depressed Ω and temperature elicit a direct negative effect upon coral calcification and reef building (Langdon et al. 2000), it is hypothesized that these two variables may be just as, if not more responsible

than nutrients for the paucity of reef development in upwelling zones.

The intensity of upwelling varies regionally and strongly influences reef development across the ETP (Cortés 1997). High-CO₂, low- Ω influenced coral reefs of the ETP are poorly cemented accretions of CaCO₃ that are subject to rapid bioerosion (Manzello et al. 2008; Fig. 2a). The thickness of these reefs reflects Ω in a positive, linear fashion (Fig. 3), illustrating the net result of coral calcification (CaCO₃ production) minus its loss (erosion) over geologic time. Fig. 3 illustrates the extent of reef framework accumulation across a naturally-occurring gradient of seawater chemistry, but does not imply a direct cause and effect relationship as there are several additional physical variables that significantly influence reef growth and development such as temperature, light, shelf-area, and antecedent topography (Macintyre et al. 1992). Despite these caveats, it can be reasonably deduced that the effects of high-CO₂ most clearly manifest over geologic time-scales in the processes of reef framework development, preservation potential, and persistence (reef cementation: Manzello et al.

2008; framework accumulation: Fig. 3), rather than in the readily observable biological phenomena on the reef surface.

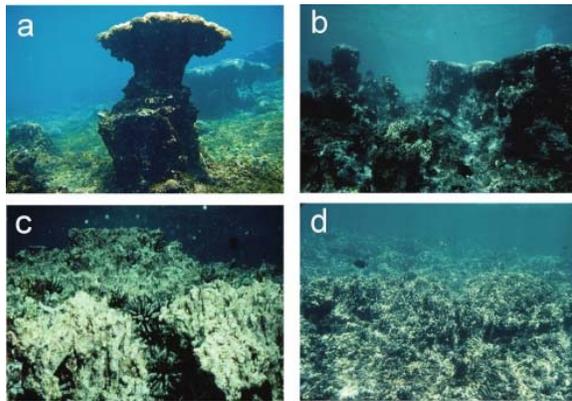


Fig. 2. **a** Typical coral reef framework structure where greatest reef development occurs in the far eastern Pacific: Secas Islands, Gulf of Chiriquí, Panamá. Vertical relief of framework structure is ≈ 1.5 m. **b** Galapagos coral reef prior to 1982-83 El Niño-Southern Oscillation (ENSO) in 1976. **c** Rapid bioerosion of dead reef framework by echinoids (*Eucidaris galapagensis*) in 1987. **d** Galapagos reef framework completely bioeroded to rubble and sediment by 1992. Images **a** and **b-d** taken by and courtesy of T. B. Smith (Univ of Virgin Is) and P. W. Glynn (RSMAS, Univ of Miami), respectively.

Ocean acidification and global warming analogs in the eastern Pacific

Anthropogenic forced climate change models predict continued and accelerated global warming due to rising concentrations of CO_2 , primarily from the unregulated combustion of fossil fuels since the industrial revolution (IPCC 2007). Global mean surface temperature has increased approximately 0.74°C in the past 100 yrs and is expected to increase by no less than 1.5°C further by the year 2100 (IPCC 2007). Proposed increases in temperature are of concern because reef-building corals live at or near their upper thermal limits as positive temperature anomalies of as little as 1°C sustained for one month during the warmest part of the year have been shown to correlate with mass-coral bleaching events (Glynn 1993; Goreau and Hayes 1994; Brown 1997).

An estimated one-third of all the CO_2 released into the atmosphere since the industrial revolution has been absorbed by the oceans (Sabine et al. 2004). This ongoing and accelerating uptake of atmospheric CO_2 is causing a drop in seawater pH at the global scale (Orr et al. 2005), resulting in an acidification of the surface ocean (Caldeira and Wickett 2003). Ocean acidification results in a decrease in seawater $[\text{CO}_3^{2-}]$ and, consequently, a decrease in the saturation state (Ω) of carbonate minerals (Kleypas et al. 1999b). Acidification is expected to reduce coral reef calcification and increase reef dissolution, and the relative rates of change will likely be a function of

pCO_2 in surface seawater, which is near equilibrium with pCO_2 in the atmosphere (Smith and Buddemeier 1992; Kleypas et al. 1999b; Langdon et al. 2000; Yates and Halley 2006). Carbonate budget studies have shown that healthy coral reefs exhibit low net accretion due to high rates of physical, chemical and biological erosion (reviewed by Glynn 1997a). Consequently, any disturbance that causes either decreased accretion or increased erosion may tip the tenuous balance from reef framework growth to loss.

The carbonate chemistry of seawater influencing reef sites in the Galapagos and Gulf of Panamá is similar to what is expected for the average tropical surface ocean with a doubling and tripling of atmospheric CO_2 , respectively (Fig. 3). Thus, the response of these reef communities to the El Niño-Southern Oscillation (ENSO) provides a real-world example of what may be the future for coral reefs globally with accelerating climate change.

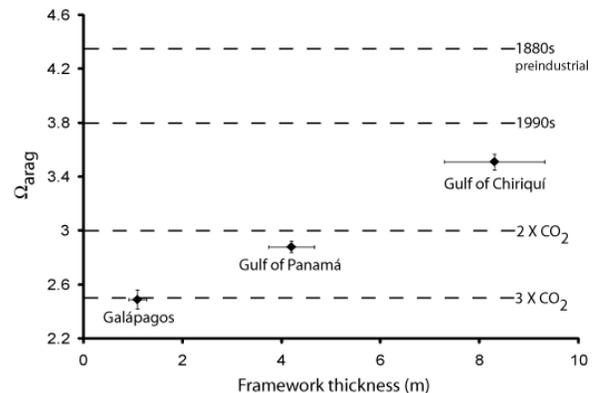


Fig. 3. Mean maximum reef framework thickness (m, \pm SEM) from eastern tropical Pacific relative to the saturation state of aragonite, Ω_{arag} . Aragonite is the type of CaCO_3 deposited by Scleractinian corals. Ω_{arag} values measured in ETP and estimated for average tropical surface ocean with differing levels of atmospheric CO_2 calculated as described in Manzello et al. (2008). Framework thicknesses of all pocilloporid reef sites prior to the 1982-83 ENSO in Galapagos and Panamá originally presented by Glynn and Wellington (1983) and Glynn and Macintyre (1977), respectively.

Galapagos coral reef communities experienced a greater and longer thermal anomaly ($3-4^\circ\text{C}$ for several months) associated with the 1982-83 ENSO in comparison to those in Pacific Panamá ($1-2^\circ\text{C}$ for two months) (Podesta and Glynn 1997). As a result, coral mortality from prolonged bleaching was greater in Galapagos (97-99%) compared to Panamá (75-85%; Glynn 1990). Following this mass mortality, reef framework structures in Galapagos were rapidly and completely bioeroded to rubble and sand in less than a decade and are now non-existent (Glynn 1994; Reaka-Kudla et al. 1996; Fig. 2b-d). Conversely, reef framework structures have persisted in Panamá despite evidence of net erosion following two severe

ENSO events (Eakin 2001). The rapid destruction and disappearance of Galápagos reefs is the end result of several cascading factors that include the extreme thermal anomaly/resultant mass mortality, less pre-existing amounts of reef framework compared to Panamá, a population explosion of bioeroding echinoids, and poor recruitment potential (Glynn 1994). However, the impact of high-CO₂, low-Ω seawater on carbonate cement precipitation and its apparent inverse relationship to bioerosion rate in the ETP adds a key piece to the puzzle as to why reefs throughout the ETP are poorly developed and ephemeral on geologic time-scales (Manzello et al. 2008).

Durham's dilemma revisited

The closure of the Panamanian isthmus 3 to 3.5 million years ago established the present-day oceanographic conditions (Keigwin 1982) necessary for ENSO-related climate phenomenon (Colgan 1990). These oceanographic conditions also established the chronic upwelling of high-CO₂, sub-thermocline waters to the surface layers throughout the ETP (Keigwin 1982; Takahashi et al. 1997; Manzello et al. 2008). Even where ETP reefs are best developed in the Gulf of Chiriquí off Panamá, the signature of these high-CO₂, low-Ω waters is evident at shallow depths (Table 1). These significant decreases in Ω, temperature, and increases in turbidity and nutrients at shallow depths illustrate why reefs are generally restricted to very shallow depths (< 10 m) throughout the ETP (Dana 1975; Glynn and Maté 1997; Cortés 1997; D'Croz and O'Dea 2007).

Table 1. Carbonate parameters measured *in situ* at surface ($n = 82$) and 15 m depth ($n = 13$) at the Uva Reef, Gulf of Chiriquí, Panamá. Values represent means (\pm SEM) of samples taken during both wet and dry seasons over four consecutive years (2003-2007).

Depth	TCO ₂ ($\mu\text{mol kg}^{-1}$)	TA ($\mu\text{mol kg}^{-1}$)	pH (sws)	pCO ₂ (μatm)	Ω_{arag}	T (°C)
< 5 m	1795.3 (9.27)	2089.6 (8.45)	8.01 (0.01)	406 (14.1)	3.51 (0.06)	28.9 (0.11)
15 m	1931.0 (18.8)	2187.5 (15.4)	7.96 (0.012)	480 (16.5)	3.05 (0.09)	25.9 (0.77)
[†] <i>P</i>	***	***	*	**	**	***

[†]-Probability that two distributions were not significantly different using Mann-Whitney *U*-tests ($P < * = 0.01$, $** = 0.001$, $*** < 0.0001$). TCO₂, TA and *in situ* temperature measured and CO₂-system calculated as described in Manzello et al. (2008).

J. W. Durham (1966) posited two questions, later referred to by Glynn (1997b) as 'Durham's dilemma', related to the depauperate state of coral reefs in the far eastern Pacific: (1) Why are coral reefs absent during the late Cenozoic and (2) why did so many genera of corals go extinct in the ETP during the Cenozoic, but continue to persist in other areas? Glynn (1997b) suggested that the ENSO-induced thermal anomalies that can elicit mass-mortalities, severe population reductions, and extirpations of reef corals throughout

the ETP were likely a pivotal element towards resolving this dilemma.

Veron (2008) recently hypothesized that perturbations to the global carbon cycle and ocean acidification provide an explanation for past episodes of reef-building extinction (i.e. reef gaps) in the geologic record. The interaction of oceanography, biology, and geology in response to ENSO across the ETP illustrates one mechanism for the cessation of reef-building and destruction of reef structures.

The chronic influence of these previously unappreciated low-pH, low-Ω, and high-pCO₂ waters acting in concert with periodic, acute ENSO-associated thermal anomalies may provide an answer to Durham's dilemma while simultaneously granting a real-world model for the combined thermal and chemical ramifications of climate change on coral reef structure (Manzello et al. 2008), function and resilience to disturbance over geologic time.

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