Effects of Global Warming and Ocean Acidification on Carbonate Budgets of Eastern Pacific Coral Reefs

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Abstract

Eastern tropical Pacific (ETP) coral reefs provide a real-world example of reef growth, development, structure, and function under the high-pCO_2, low aragonite saturation state (Ω_{arag}) conditions expected for the entire tropical surface ocean with a doubling to tripling of atmospheric CO_2. This provides a unique opportunity to examine various aspects of calcium carbonate ($CaCO_3$) budgets in low-Ω_{arag} conditions in the present day. Unlike anywhere else in the world, the ETP displays a continuum of thermal stress and CO_2 inputs up to levels at which reef building is terminated and reef structures are lost. The response of coral reef $CaCO_3$ budgets to El Niño warming across the ETP shows that reefs can be completely lost after experiencing a 2–3 °C thermal anomaly sustained in excess of two months during the warmest time of the year at Ω_{arag} values expected for the rest of the tropics when atmospheric CO_2 doubles. ETP coral reefs have persisted and shown resilience to this level of thermal stress or acidification when acting alone, but the combination of the two corresponded with the complete elimination of reef framework structures in the southern Galápagos Islands over the decade after the 1982–83 El Niño warming event. Reef carbonate degradation is exacerbated also by diverse agents of bioerosion such as sea urchins, boring bivalves, and excavating sponges, with experimental evidence demonstrating that the latter may even increase their activities during ocean warming and pH decline. This chapter reviews the $CaCO_3$ budget of ETP coral reefs and discusses how a high-CO_2 world may impact the major biotic and abiotic factors responsible for the cycling of carbonate materials. Coral reefs of the ETP serve as a model for conditions that will occur in other regions within a few decades.

Keywords

Climate change • Aragonite saturation state • Calcification • Bioerosion • Thermal stress

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18.1 Introduction

The first scientists to visit the eastern tropical Pacific (ETP), including Charles Darwin, commented on the apparent absence of reef development (Darwin 1842). Structural reefs were later discovered and found to have rapid accretion rates over the past 5600 years, rivaling Holocene reef accretion rates elsewhere (Glynn et al. 1972; Glynn and Macintyre 1977; see Chap. 6, Toth et al.). Despite rapid accretion at a few protected sites, ETP reefs are highly porous, uncemented accumulations of calcium carbonate ($CaCO_3$) relative to those in the Indo-Pacific and Caribbean. They are generally small in areal extent (usually a few hectares), limited to shallow depths (<15 m), patchily distributed, and likely ephemeral on geologic time scales (Glynn et al. 1972; Dana 1975; Manzello 2009). This poor coral reef development in the ETP is thought to be a consequence of multiple stresses that place them at the edge of suitable environmental conditions for reef accretion: colder temperatures and high turbidity from frequent upwelling (Dana 1975) and El Niño-related climate variability (Glynn and Colgan 1992). Recently, it has been appreciated that these reefs are also exposed to chronic high-pCO_2 conditions as a result of upwelling and thermocline shoaling that depresses the saturation state of aragonite (Ω_{arag}) throughout the ETP (Manzello et al. 2008).

18.2 Climate Change

18.2.1 Ocean Warming

Climate change models forced with anthropogenic greenhouse gases predict continued and accelerated global warming due to rising concentrations of CO_2, primarily from the combustion of fossil fuels since the industrial revolution (IPCC 2013). Global mean surface temperature has increased ~0.85 °C during the period 1880–2012 and is expected to increase by 2.6–4.8 °C under Representative Concentration Pathway (RCP) 8.5—the worst case scenario in the latest IPCC report, which has emission rates at or below current levels of atmospheric CO_2 and emission acceleration (IPCC 2013). Proposed increases in temperature are of concern because reef-building corals live at or near their upper thermal limits. Positive ocean temperature anomalies of as little as 1–2 °C sustained for one to two months during the warmest part of the year correlate with mass-coral bleaching and mortality events (Glynn 1993; Goreau and Hayes 1994; Brown 1997; Berkelmans 2002) and such temperature anomalies have been shown experimentally to reproduce this bleaching and mortality (Glynn and D'Croz 1990; Berkelmans and Willis 1999). It is expected that continued warming will increase both the frequency and severity of thermal stress and bleaching events over the next century (Hoegh-Guldberg 1999; Donner et al. 2005, 2009; Logan et al. 2014; van Hooidonk et al. 2014). Thermal stress events and resultant mass coral bleaching have indeed become more severe and widespread over the past 20–30 years (Baker et al. 2008; Eakin et al. 2009), lending support to the notion that reef communities are already being severely impacted by warming (e.g., Eakin et al. 2010).

The response of ETP coral reefs to warming associated with the El Niño-Southern Oscillation (ENSO) is a cornerstone in the understanding of the effects of climate change on coral reefs (e.g., Hughes et al. 2003). The first warning signs of global warming impacts on coral reef ecosystems manifested in the ETP (Glynn 1983, 1984, 1991). While some disregarded these observations when first presented, the deleterious effects of climate change on coral reefs have now been labeled as 'incontrovertible' (Hughes et al. 2003) and are widely accepted as one of the leading threats to the persistence of coral reefs (Kleypas and Eakin 2007). The IPCC (2014) has identified coral reefs as one of the marine ecosystems most vulnerable to damage from climate change.

18.2.2 Ocean Acidification

The oceans have taken up approximately 30 % of the anthropogenic CO_2 released into the atmosphere since the industrial revolution (Sabine et al. 2004; Orr et al. 2005; Le Quéré et al. 2009), causing an acidification of the surface ocean in equilibrium with the lower atmosphere (Caldeira and Wickett 2003). Ocean acidification (OA) decreases the concentration of the carbonate ion in seawater $[CO_3^{2-}]$ and, consequently, decreases the saturation state of carbonate minerals ($\Omega = [CO_3^{2-}][Ca^{2+}]/K'_{sp}$, where K'_{sp} is the solubility product for a carbonate mineral). Acidification is expected to depress coral reef calcification, increase reef dissolution and bioerosion, and reduce reef resilience (Kleypas et al. 1999; Yates and Halley 2006; Tribollet et al. 2009; Anthony et al. 2011)—making coral reefs, along with Arctic ecosystems, one of the two ecosystems considered at greatest risk to ocean acidification (IPCC 2014). Despite these concerns, our understanding of how the combined effects of warming and OA will alter the structure and function of coral reef ecosystems is rudimentary.

Surface waters in many parts of the ETP have lower pH, lower Ω_{arag}, and higher pCO_2 (the partial pressure of CO_2) values relative to other tropical waters because CO_2-enriched deep waters are upwelled to the surface layers along the shallow thermocline (Fig. 18.1) (Takahashi et al. 1997;

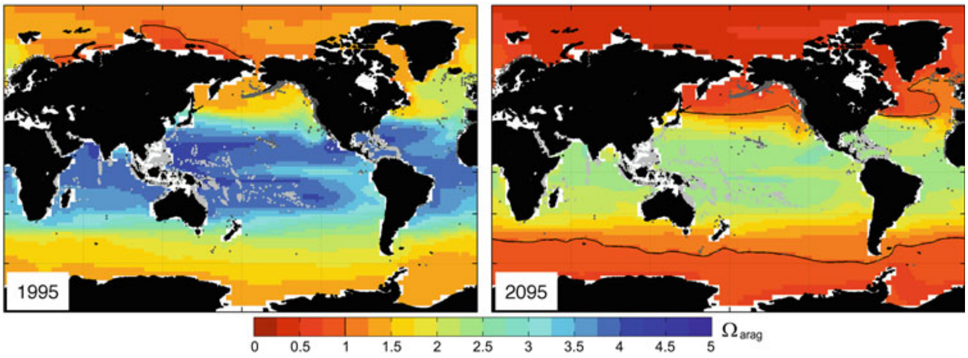

Fig. 18.1 Predicted Ω_{arag} values with increasing atmospheric CO_2 (ppm). Adapted from Feely et al. (2009)

Manzello et al. 2008; see Chap. 3, Fiedler and Lavín). The intensity of this upwelling varies regionally and strongly influences reef development across the ETP (reviewed by Cortés 1997). This unique oceanography of the ETP makes it an exemplary natural laboratory to study the effects of high-pCO_2 conditions on coral reef ecosystem processes and responses to disturbance (Manzello 2009). While other high-pCO_2 tropical reef sites are known in the Pacific (e.g., Jarvis, Line Islands and CO_2 seeps at Maug in the Mariana Islands and Papua New Guinea), these sites are poorly characterized and lack the long-term ecological understanding of the ETP sites (e.g., Fabricius et al. 2011 in contrast with Glynn et al. 2001). Bermuda experiences the lowest Ω_{arag} values in the Atlantic because it is a high-latitude reef system that experiences seasonally low temperatures but the typical values there ($\Omega_{arag} \geq 3$: Bates et al. 2009) are still greater than most ETP reef sites (Manzello 2010a). Some of the lowest known Ω_{arag} values ever documented for any coral reef site in the world are those from the Galápagos Islands (Manzello et al. 2008; Manzello 2010a).

ETP coral reefs provide a real-world example of reef growth, development, structure and function under high-pCO_2, low-Ω_{arag} conditions that encompass the range of expected changes for the entire tropical surface ocean with a doubling to tripling of atmospheric CO_2 (Fig. 18.1) (Manzello et al. 2008; Manzello 2009, 2010a). Reef structural development is highly limited in the marginal low-Ω_{arag} environment of the ETP and, perhaps most striking, ephemeral on geologic timescales (Glynn and Colgan 1992; Macintyre et al. 1992). These high-pCO_2 ETP reefs have been instrumental to understanding the anticipated impacts of OA on coral reefs in the real-world (see discussion of ETP reefs in Cohen and Holcomb 2009; Doney et al. 2009; Hofman et al. 2010; Hoegh-Guldberg 2011; Pandolfi et al. 2011, and others). The naturally high-pCO_2 of the ETP causes reefs in this region to persist near the Ω_{arag} distributional threshold for coral reefs (Kleypas et al. 1999). As a result, these high-pCO_2 reefs are ocean acidification 'hotspots' because they may: 1) display the first negative effects of, and 2) be the most affected by rising CO_2 levels (Manzello et al. 2008; Manzello 2010a). It must be noted that the ETP will experience the most modest oceanic decrease in Ω_{arag} owing to the already very low Ω_{arag} and large natural variability of this region due to effects of upwelling and ENSO on carbonate chemistry (Friedrich et al. 2012). It is possible that the high natural variability and chronically low Ω_{arag} of the ETP could already have led to adaptation to high pCO_2, possibly making resident organisms more tolerant to future acidification. The rate and magnitude of change in Ω_{arag} due to ocean acidification also is important to the impact experienced by organisms. Locations like the Caribbean Sea, despite currently having higher absolute Ω_{arag} values than the ETP, will experience a larger magnitude and rate of change in Ω_{arag} with ocean acidification (Friedrich et al. 2012). Regardless, the ETP will always have the lowest Ω_{arag} values of the tropics. Thus, if there are critical threshold values of Ω_{arag} to reef function, ETP reefs will be the first to cross that value, and may arguably have already done so in certain locations like the southern Galápagos Islands and for certain reef processes.

18.3 Coral Reef Carbonate Budget

18.3.1 $CaCO_3$ Production

There are many calcifying organisms that inhabit coral reefs. Some $CaCO_3$ production contributes to the reef framework (e.g., reef building corals and crustose coralline algae), some to reef sediments [e.g., detrital skeletal material, some articulated calcareous algae (e.g., *Halimeda*)], and some to coating and binding reef materials (e.g., encrusting coralline algae). Corals are generally the largest producers of reefal $CaCO_3$ and serve as the major building blocks of reef framework accumulation (Scoffin et al. 1980; Hubbard et al. 1990; Eakin 1996; Macintyre 1997). An exception to this can be found in environments where corals are unable to live, or where their skeletal remains cannot accumulate into reef framework structures, such as high surge environments like algal ridges (Adey 1978; Grigg 1998). Crustose coralline algae (CCA) also may opportunistically expand to cover space after coral mortality (Eakin 1992) and can indeed cover large areas of reef framework (Eakin 1992, 1996). Frequently, while non-coral $CaCO_3$ production by certain organisms can be quite high, (e.g., *Halimeda*: Rees et al. 2007), the majority of this $CaCO_3$ production generally ends up in the sediment aprons that flank reef frameworks and infilling reef cavities, and does not contribute significantly to the buildup of the rigid, three-dimensional wave resistant structure of the reef unless bound by cements (Orme 1977; Hubbard et al. 1990). CCA, bryozoans, vermetid gastropods, barnacles, and non-boring bivalves can encrust reef frameworks and contribute to the carbonate budget—in some cases becoming major parts of the overall reef carbonate budget. As in most other coral reefs, the carbonate production rates and contribution to reef framework building of these organisms are lower than corals in the ETP (Glynn and Macintyre 1977; Macintyre et al. 1992; Cortés et al. 1994; Eakin 1996).

Another source of $CaCO_3$ production on coral reefs is carbonate cementation. Cementation is the precipitation of $CaCO_3$ that acts to bind framework components and occlude porosity (Perry and Hepburn 2008). The precipitation of much of the aragonite cement in reef environments was originally thought to be inorganic, or abiotic, driven by the carbonate supersaturation of reef waters, but this is still debated (Nothdurft and Webb 2009). The distribution of most other cement types (i.e., high-mg calcite cements) within coral skeletal pores and reef rock suggests that their precipitation is a result of direct microbial precipitation or microbially mediated microenvironments, although broader scale physico-chemical control likely plays an important role (Nothdurft and Webb 2009). For example, endolithic algae are a nearly ubiquitous feature of coral skeletons living directly below the live coral tissue layer that, through photosynthetic CO_2 removal, may facilitate the precipitation of calcium carbonate cements. The high-energy seaward margins of exposed oceanic reefs are usually the most cemented reef formations and cement abundance decreases (often to zero) as water motion decreases across reef crests and into inner shelves and lagoons (James et al. 1976; James and Ginsburg 1979). $CaCO_3$ does precipitate inorganically outside of high-flow areas (e.g., lagoonal environments), but these precipitates usually form unlithified mud that does not bind substrate components (Macintyre and Aronson 2006).

Many processes, particularly those biogeochemical processes that affect reef porewater chemistry, influence reef cementation (James et al. 1976; James and Ginsburg 1979; Macintyre and Marshall 1988; Tribble et al. 1992; Tribble 1993; Rasser and Riegl 2002; Perry and Hepburn 2008). Advection of seawater supersaturated with respect to $CaCO_3$ into reef frameworks is considered a prerequisite for extensive cementation (Buddemeier and Oberdorfer 1986; Tribble et al. 1992). As a result, anthropogenic acidification may reduce future cement precipitation (Andersson et al. 2003) by reducing Ω_{arag} in the oceanic waters bathing reefs. Those cements composed of the more soluble high-mg calcite phase of $CaCO_3$ are expected to be most affected by OA (Andersson et al. 2008). Indeed, $CaCO_3$ cements do not currently precipitate above trace levels in the ETP (Fig. 18.2) (Manzello et al. 2008) and are not found in fossil sediments for the last several thousand years (Glynn and Macintyre 1977). Concomitantly, rates of bioerosion in the ETP are the highest measured anywhere in the world (Manzello et al. 2008; see Chap. 12, Alvarado et al.).

Processes of construction and destruction are often closely balanced on coral reefs (Glynn and Manzello 2015). As such, any disturbance that impairs coral growth can potentially drive coral reefs into a state of degradation. Coral mass mortality

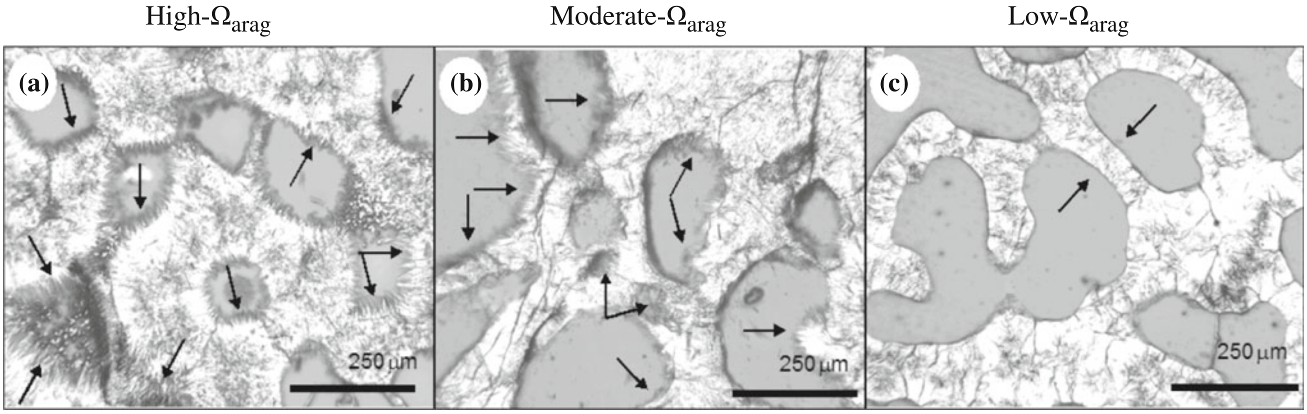

Fig. 18.2 Thin-section photomicrographs of cement distributions. **a** Abundant cementation in the intraskeletal cavities of a coral from high-Ω_{arag} environment in Bahamas ($\Omega_{arag} > 4$). *Arrows point* to examples of aragonite cement crystals. **b** Example of most heavily cemented sample from moderate-Ω_{arag} in Panama. **c** Sample from low-Ω_{arag} Galápagos ($\Omega_{arag} < 3$), in which cement is absent from all intraskeletal pores. From Manzello et al. (2008, © PNAS)

events illustrate a tipping point in the dynamics between reef construction and destruction; as such disturbances are usually followed by a decline in topographic complexity and can even result in the loss of framework structures (Alvarez-Filip et al. 2009; Manzello 2009). Such structural degradation was observed in Panama and the Galápagos Islands after the 1982–83 El Niño event (Glynn 1988; Eakin 2001).

18.3.2 $CaCO_3$ Loss

18.3.2.1 Bioerosion

The breakdown and erosion of coral skeletons and reef framework structures by the activities of organisms is termed bioerosion (Neumann 1966). Bioerosion is a fundamental process that can strongly limit the growth rates and patterns of coral reef development and sustainability if the balance between constructional and destructional processes is altered (Goreau and Hartman 1963; Risk and MacGeachy 1978; Scoffin et al. 1980; Hutchings 1986; Tribollet and Golubic 2005). There are a wide variety of organisms that bioerode coral reef carbonates. These organisms have been characterized according to whether they live externally or internally within calcareous structures, their mechanisms of bioerosion (e.g., grazers, borers, scrapers), and the size of the responsible organism (e.g., macro- vs. microborers; see Chap. 12, Alvarado et al.).

Sea urchins are external bioeroders that play a significant role in the ETP (Glynn et al. 1979, 2015; Glynn 1988; Eakin 1996). The long-spined (*Diadema mexicanum*) and pencil-spined sea urchins (*Eucidaris galapagensis*) are the dominant eroders in terms of $CaCO_3$ degradation per unit area in Panama and the Galápagos Islands, respectively (Glynn et al. 1979; Eakin 1996). The corallivorous pufferfish, *Arothron meleagris*, is also an external bioeroding agent on ETP reefs, but contributes less to the total $CaCO_3$ breakdown on these reefs (Glynn et al. 1972; Guzmán and Robertson 1989; Palacios et al. 2014). Recent research has shown that corallivory by *A. meleagris* can remove up to 16 % of the annual carbonate produced by pocilloporid corals (Palacios et al. 2014). Bioerosion by other fishes on ETP reefs (e.g., scarids, balistids, monacanthids) plays only a minor role in the $CaCO_3$ budget (Eakin 1996).

An entire community of other eroders lives and produces sediment within branching coral frameworks. This community includes internal eroders such as clionaid sponges, endolithic algae, polychaetes, sipunculans, and lithophagine bivalves, and external eroders such as polychaetes, gastropods, and crustaceans. These organisms contributed equally to sediment production as echinoids during erosion experiments in the Galápagos and Panama (Glynn 1988) and were the largest biogenic source of sediment in carbonate budgets in Panama (Eakin 1996).

Among the intraskeletal bioeroders, boring bivalves are recognized as having the greatest impact at several ETP sites (Cantera et al. 2003; Londoño-Cruz et al. 2003; Fonseca et al. 2006; see Chap. 12, Alvarado et al.). *Lithophaga* spp. bivalves can be highly abundant in the ETP, primarily within the skeleton of the coral *Porites lobata*, but also in *Pocillopora* spp. In the ETP, these boring molluscs achieve the highest densities (100s of individuals per m^2 surface area; Scott et al. 1988; Kleemann 1990, 2013) that have ever been documented, where they significantly compromise the integrity and strength of the skeleton they bore into (Scott and Risk 1988) and where feeding on them by triggerfish can cause significant coral fragmentation (Guzmán and Cortés 1989; see Chap. 15, Glynn et al.). Polychaete worms can also be locally abundant within massive pavonid corals in the ETP (Manzello, pers. obs.). Boring sponges (e.g., *Cliona* spp.), which can be dominant agents of $CaCO_3$ breakdown in other geographic areas like the Caribbean (Neumann 1966; Scoffin et al. 1980), appear to play a more limited role in the ETP (Scott et al. 1988; Carballo et al. 2008). This is somewhat paradoxical given that these organisms are thought to be stimulated by elevated nutrient levels (Risk and MacGeachy 1978; Rose and Risk 1985) and upwelling is a source of elevated nutrient concentrations throughout the ETP (D'Croz and O'Dea 2007). In general, there is confusion as to the importance of internal boring organisms as their numbers can dramatically vary in abundance across reef zones and from reef to reef (Macintyre 1984). Recently, the importance of endolithic algae in the process of bioerosion has been recognized (Tribollet et al. 2002; Tribollet and Golubic 2005). The role of these important bioeroders deserves further attention in the ETP, especially given that their rate of dissolution is stimulated by OA (Tribollet et al. 2009; Fang et al. 2013, 2014).

18.3.2.2 Physical Erosion (Wave Energy, Storms)

The majority of coral reefs in the ETP exist in sheltered environments and are not exposed to high levels of wave energy (see Chap. 6, Toth et al.). As such, physical erosion of $CaCO_3$ reef structures is, at best, an episodic occurrence in the ETP that is limited only to the strongest storm events. Furthermore, most ETP reefs occur outside of the tropical cyclone belt, but occasionally tropical storms can affect reef communities (e.g., Lirman et al. 2001). Nevertheless, physical disturbance can be relegated to a minor role in the breakdown and destruction of ETP reef framework structures.

18.3.2.3 Chemical Erosion (Dissolution)

A global model of carbonate production showed that most coral reefs could experience net dissolution with a doubling of atmospheric CO_2 due to expected declines in calcification, even if rates of dissolution do not change with acidification (Silverman et al. 2009). It has been suggested that reef dissolution will increase via the enhancement of pore-water acidity within reef frameworks and sediments as OA progresses (Yates and Halley 2006). Kinsey (1978) pointed out, however, that rates of reef dissolution are erratic, unpredictable, and highly variable. As such, we currently have a very limited understanding of the overall magnitude that purely chemical dissolution plays in reefal $CaCO_3$ in general, and especially among ETP reefs. The dissolution signal measured in bulk seawater overlying coral reefs at night is driven, to some unknown extent, by those organisms that chemically erode carbonate (e.g., *Lithophaga*: Lazar and Loya 1991; *Cliona*: Fang et al. 2013; Wisshak et al. 2013). Preliminary data show that dissolution does occur within pore-waters of the Uva Island reef in Pacific Panama, but it still isn't clear how this relates to other reefs, if the naturally high-pCO_2 stimulates this process, or if it is inherently controlled by the oxidation of organic matter (e.g., Tribble 1993). This is a fruitful area for future research in the ETP and on reefs across the globe.

18.3.3 Carbonate Budgets of the ETP

Rapid growth of pocilloporid corals provides a competitive advantage for space on ecological timescales, while the high skeletal density of these corals imparts a greater preservation potential on geologic timescales. These traits help explain why pocilloporid corals are often the dominant reef builders throughout the ETP (Cortés 1997; Glynn and Maté 1997). The best developed reefs in the ETP occur off the Pacific coast of Panama in the nonupwelling Gulf of Chiriquí (Glynn and Macintyre 1977; Macintyre et al. 1992). Not surprisingly, rates of carbonate production by pocilloporid corals in this region are among the highest reported in the ETP, only exceeded by more recent reports from Mexico. Estimated coral carbonate production rates for the Uva Island reef, in the Gulf of Chiriquí, ranged from 64.4 to 67.2 tonnes ha^{-1} $year^{-1}$ (Table 18.1). The Secas reef, also in the Gulf of Chiriquí, revealed a similar production rate of 67 tonnes ha^{-1} $year^{-1}$. The production rates for corals in the upwelling Gulf of Panama were about 30 % (Señorita reef) and 75 % (Saboga reef) of those reported under nonupwelling conditions in the Gulf of Chiriquí.

Coral carbonate production rates demonstrate high inter-annual variability, which is evident from estimates determined at the Cabo Pulmo reef for three periods from 1987 to 2012 (Table 18.1). The carbonate production rates ranged from low values of 17–39 tonnes ha^{-1} $year^{-1}$ in 2003 to high values of 89.5–203.6 tonnes ha^{-1} $year^{-1}$ in 1987. The very high rates of production in Mexico are based on areas of the reef with very high coral cover and may overestimate whole-reef production (Calderon-Aguilera, pers. commn.). We expect that reef- scale carbonate production tracks SST and Ω_{arag} across the wider ETP, as it does in Panama and Galápagos (Manzello et al. 2008, 2014). Individual coral calcification rates and overall population-level $CaCO_3$ production of the coral species *Porites panamensis* is indeed positively and linearly related to SST in Mexico (Nozagaray-López et al. 2014). Other large differences are related to reductions in live coral cover, a result of severe coral mortality caused by thermal bleaching and physical storm damage. The significant declines in production after 1987 were attributed to the 1997 El Niño warming event and Hurricane Isis in 1998 (Calderón-Aguilera et al. 2007). A large increase in carbonate production by 2012 was accompanied by an increase in live coral cover, a result of community recovery. Three other coral reefs on the Mexican mainland (Chimo, Tenacatita, and La Entrega) demonstrated similar inter-annual differences in carbonate production depending on variations in local live coral cover levels (Table 18.1).

The $CaCO_3$ budgets of ETP reefs are highly dynamic, with many reefs switching from net deposition before to net erosion following the 1982–83 ENSO-related mass mortality of corals (Glynn 1988; Eakin 1996; Reaka-Kudla et al. 1996). Additionally, the lack of cementation has produced reefs consisting of fragile stacks of coral skeletons. In fact, many reef structures in the Galápagos Islands were completely eroded down to the antecedent basalt foundation in less than a decade (Glynn 1994; Manzello 2009). Reef structures have persisted in Panama, despite the switch from net construction to net erosion following two severe ENSO events (Eakin 1996, 2001). Figure 18.3 shows a diagrammatic budget for the solid-phase $CaCO_3$ in the Uva reef system before and after the extensive bleaching caused by the 1982–83 El Niño. The major erosion that followed the 1983 coral bleaching and mortality in Panama did, however, convert a large section of the Uva reef structure to sediment, converting reef framework to a sandy plain (Eakin 2001). It is important to note that each El Niño event has a very different downstream effect. While the 1997–98 event has been argued by some to be the largest El Niño in the historical record (Wolter and

Table 18.1 Coral carbonate production rates across the eastern tropical Pacific

Study Site		Species-composition	Live coral cover (%)	Production[a] metric tons ha^{-1} year^{-1}	Authority
Cabo Pulmo Mexico	23°25′N	*Pocillopora, Porites, Pavona, Psammocora*	62	89.5–203.6 (1987)	Reyes-Bonilla (1993)
			12	17–39 (2003)	Calderón-Aguilera et al. (2007)
			25.7	68 (2012)	Reyes-Bonilla et al. (2014)
Chimo Mexico	20°2′N	*Pocillopora*	5.4–6.2	9.2–20.0 (2003)	Calderón-Aguilera et al. (2007)
Tenacatita Mexico	19°16′N	*Pocilliopora*	52.9	88.8–204.0 (2003)	Calderón-Aguilera et al. (2007)
La Entrega Mexico	15°45′N	*Pocillopora*	40.9	65.5–150.5 (2003)	Leyte-Morales (2001)
Saboga Is Panamá	8°38′N	*Pocillopora, Pavona, Porites, Gardineroseris, Psammocora*	45–55	51 (1971)	Glynn (1976) Glynn (1977)
Señorita Is Panamá	8°27′N	*Pocillopora*	25–30	20.5 (1971)	Glynn et al. (1972)
Secas Is Panamá	7°57′N	*Pocillopora*	34	67 (1972)	Glynn et al. (1972) Glynn (1976)
Uva Is Panamá	7°49′N	*Pocillopora,*	36–39	64.4 (pre-1983)	Wellington and Glynn (2007)
		Gardineroseris, Psammocora	25.4	67.2 (post-1983)	Eakin (1996)
Gorgona Is Colombia	2°58′N	*Pocillopora*	49.6	56	Palacios et al. (2014)
Devil's Crown Galápagos	1°12′S	*Pocillopora,*	10	10 (1975–1976)	Glynn et al. (1979)
		Porites, Pavona, Psammocora	50	55	
Floreana Is Galápagos	1°16′–1°19′S	*Pocillopora Porites, Pavona, Psammocora*	0.91	0.082 (2000–2001)	Bustamante et al. (2008) Okey et al. (2004)

[a]Minimum and maximum production values are indicated for Mexican sites. Years sampled are noted in parentheses

Timlin 1998; McPhaden 1999; Wang and Weisburg 2000), warming patterns in the eastern tropical Pacific were quite different than those in 1982–83, resulting in less coral bleaching in Panama (Glynn et al. 2001). The rapid destruction and disappearance of Galápagos reefs is the end result of several cascading factors that include the extreme thermal anomaly with its resultant mass coral bleaching and mortality, less preexisting amounts of reef framework compared to Panama, persistent high abundances and concentration of bioeroding echinoids, and poor sexual recruitment by corals (Glynn 1994). The role of high-$p\mathrm{CO}_2$, low-Ω seawater that minimizes carbonate cement precipitation and facilitates bioerosion in the ETP together add 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).

18.4 ETP Carbonate Budgets with Warming and Acidification

18.4.1 Effects of Warming/Bleaching on $CaCO_3$ Budget: Acute, Pulse Stressor

To date, thermal stress has been an acute disturbance that has occurred with approximate ENSO periodicity in the ETP. An *acute*, or *pulse* stressor is a single, short-term disturbance that alters the environment (Connell 1997). In contrast, a *chronic*, or *press* stressor is a condition that persistently alters the environment. Acute thermal stress and bleaching are known to reduce coral skeletal extension and calcification (Goreau and Macfarlane 1990; Leder et al. 1991; Manzello et al. 2015a, b). In the best-case scenario, ocean warming will negatively affect $CaCO_3$ production due to

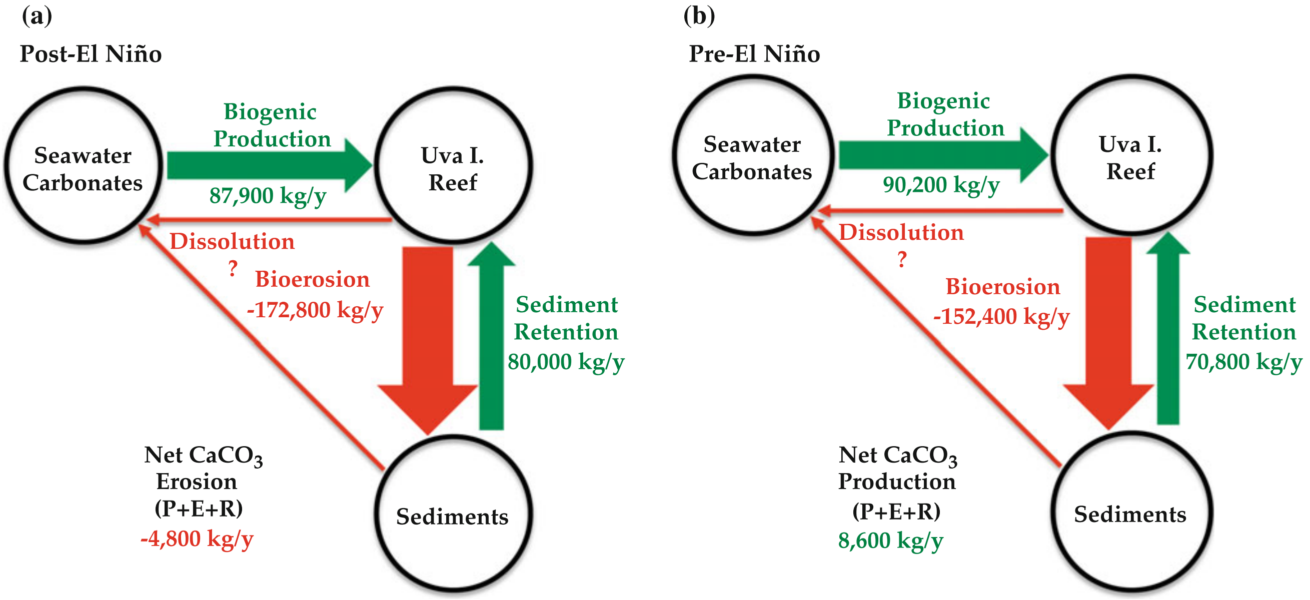

Fig. 18.3 Graphical diagram of $CaCO_3$ fluxes in Uva Island coral reef system, showing flux values from model (rounded to 100 kg/y). **a** Budget after extremely strong 1982–83 El Niño. **b** Budget prior to extremely strong 1982–83 El Niño. Positive fluxes and values in *green*; negative fluxes and values in *red*. Width of *arrows* is proportional to magnitude of fluxes. After Eakin (1996)

depressions in coral growth. If the frequency of thermal stress events increases or if temperatures surpass the optimal range for coral growth, warming would then act like a chronic disturbance, perennially reducing growth. In fact, one potential "nugget of hope" identified for corals is the switching or shuffling of zooxanthellae to clades that are more resistant to thermal stress (e.g., Baker 2001, see Chap. 13, Baker et al.). Thermally-resistant zooxanthellae, such as Clade D *Symbiodinium*, are less productive than other clades (Stat and Gates 2011). Such symbiont switching or shuffling as a response to a warming climate is likely to slow coral growth (Little et al. 2004) and reduce coral fitness (Jones and Berkelmans 2011). Additionally, the growth and calcification of corals and coral reefs will decline due to mortality associated with thermal stress, regardless of acidification.

While most coral species, including the major reef builders, have regained their former abundances in Panama since the 1982–83 El Niño, one species may have been driven to extinction. *Millepora boschmai* is a species of hydrocoral in the ETP that may have already suffered extinction as a result of thermal stress-induced bleaching (Glynn 2011). It was originally believed extinct after the 1982–83 El Niño (Glynn and de Weerdt 1991), but a small population was later located (Glynn and Feingold 1992). This remnant population died during thermal stress from the 1997–98 El Niño event (Glynn et al. 2001). In total, three hydrocorals (*Millepora platyphylla, M. boschmai, M. intricata*) and three scleractinians (*Pavona chiriquiensis*, *Porites panamensis, Gardineroseris planulata*) experienced presumed extinctions, local extirpations or severe reductions in abundances in the ETP following the 1982–83 and 1997–98 ENSOs (Glynn et al. 2001). Remnant patches of *G. planulata* that survived the 1982–83 ENSO in the Galápagos Islands also disappeared following the 1997–98 event, causing local extinctions (Glynn et al. 2001). While *G. planulata* is a significant reef-builder on some ETP reefs, most of those driven to extinction or extirpation were not. Even so, the potential for the extirpation or extinction of species from ETP reefs points to the impact that high temperatures can have on corals and even the extinction of coral species in general (Brainard et al. 2013).

18.4.2 Effects of Acidification on $CaCO_3$ Budget: Chronic, Press Stressor

Unlike thermal stress, OA is a chronic disturbance. The majority of research indicates that coral calcification will decline as a function of increasing atmospheric CO_2 (e.g., Langdon and Atkinson 2005). Yet the response to high-pCO_2 is not equal for all coral species, with some species being more tolerant to high-pCO_2 conditions than others in both laboratory and field studies (Langdon and Atkinson 2005; Manzello 2010b; Rodolfo-Metalpa et al. 2011; McCulloch et al. 2012). High-pCO_2 and temperature may interact such that the effects of high-pCO_2 do not manifest at low temperatures or the effect of one variable is exacerbated by the other (Reynaud et al. 2003; Anthony et al. 2008; Rodolfo-Metalpa et al. 2011). Growth declines may not begin until a threshold temperature is reached or exceeded. This, or perhaps the ability of some coral species to better up-regulate the pH of their calcifying fluid than others (McCulloch et al. 2012), may explain why declines in massive coral growth have not been observed in some field studies despite rising pCO_2 (Helmle et al. 2011; Cooper et al. 2012). Heterotrophic feeding and elevated nutrients may counteract the effect of declining Ω over some unknown, but limited range providing some degree of optimism as OA progresses (Cohen and Holcomb 2009). The relatively nutrient rich waters of the ETP may foster enhanced heterotrophy or fertilization of endosymbiotic zooxanthellae, enhancing coral calcification in waters that might otherwise have sub-optimal Ω_{arag} for reef growth (Manzello et al. 2014).

In addition to the effects on calcification, there is evidence that reduced pH has a negative effect on coral reproduction, with impacts on fertilization, larval settlement, and growth (Albright et al. 2010) and additionally on larval oxygen consumption and metamorphosis (Nakamura et al. 2011). Impaired recruitment reduces long-term reef growth, especially during recovery from disturbance. Sexual recruitment has been observed to be especially low in the ETP (Glynn et al. 1991, 2011; Glynn and Fong 2006).

Coral growth rates have declined over the past 30 years in the western Pacific, ETP, Indian, and North Atlantic Oceans (Edmunds 2007; Bak et al. 2009; De'ath et al. 2009; Tanzil et al. 2009; Manzello 2010b). *Pocillopora damicornis* has undergone a significant decline in growth at the Uva reef in Panama at a similar rate (approximately 1 % $year^{-1}$) to that documented in two independent studies from the Great Barrier Reef and Thailand (Manzello 2010b). Not all species of coral in Panama, however, have exhibited growth declines (Manzello 2010b).

Selection for thermally tolerant symbionts by ENSO-related bleaching may be causing or contributing to declines in the growth rates of certain species of corals (Manzello 2010b). For instance, pocilloporid corals have shown an increased tolerance to recurrent thermal stress events in Panama because they more frequently host thermo-tolerant symbiotic algae (Glynn et al. 2001; see Chap. 13, Baker et al.). Massive pavonid corals have shown less tolerance to thermal stress presumably because of less flexibility in hosting resistant algal endosymbionts (Glynn et al. 2001). The cost of this increased temperature tolerance in the Pocilloporidae, however, may be a more rapid decline in growth rate than what is anticipated from acidification. Growth rates of *P. damicornis* are correlated with Ω_{arag} across the ETP (Glynn 1977; Manzello 2010b). Conversely, massive pavonid corals have extension rates as high or higher in low-Ω_{arag} environments, which suggests that these species may be more tolerant to acidification than the Pocilloporidae. These differing sensitivities to thermal stress and ocean acidification will be a fundamental determinant of eastern tropical Pacific coral reef community structure with accelerating climate change that has implications to the future of reef communities worldwide.

The biologically-mediated dissolution of $CaCO_3$ by both clionaid sponges and endolithic algae is enhanced by OA (Tribollet et al. 2009; Wisshak et al. 2012; Fang et al. 2013, 2014; Reyes-Nivia et al. 2013; Enochs et al. 2015). Tribollet et al. (2009) found that filaments of the ubiquitous endolithic boring alga, *Ostreobium querkettii*, were able to penetrate deeper into coral rock substrates under high-CO_2 conditions, leading to an increase in $CaCO_3$ dissolution. Reyes-Nivia et al. (2013) observed increases in endolith biomass and respiration during combined exposure to elevated CO_2 and temperature, which led to increases in dissolution. These workers found a significant effect of substrate, as skeletons of the coral *Porites cylindrica* exhibited an increase in the relative abundance of *O. querkettii* within the endolithic community and a greater increase in endolith bioerosion when compared to the denser *Isopora cuneata*. This is intriguing as previous research has indicated that internal bioerosion increases with skeletal density (Highsmith 1981; Schönberg 2002), but the response with climate change and OA may differ and could follow an opposite pattern.

The increase in dissolution by endolithic algae, specifically *Ostreobium* with decreasing seawater pH, may also have implications for carbonate cementation of coral reefs. *Ostreobium* growth initiates endolithically within $CaCO_3$ crystals, but can later become chasmolithic (living inside cavities not of their own making) or epilithic, growing outside of the substrate and extending into the surrounding seawater (Kobluk and Risk 1977a). Following the death of the epilithic algal filaments, they can become completely calcified and this can occur within 2–3 months of substrate infestation (Kobluk and Risk 1977a, b). These calcified filaments can then coalesce to form a cement envelope that was hypothesized to reduce intergranular porosity and bind grains. This process differs from the infilling of vacated microborings by detrital or precipitated micrite (e.g., Bathurst 1966), as only external dead filaments become calcified, whereas those within borings do not.

Given that ocean acidification stimulates the growth of *Ostreobium* (Reyes-Nivia et al. 2013), it could be argued that acidification may promote cementation rather than depress it as has previously been suggested (Manzello et al. 2008) vis-à-vis the micritization process described by Kobluk and Risk (1977a, b). This is an intriguing proposition that deserves further investigation, yet by this rationale it seems that eastern Pacific coral reefs should be heavily cemented. Though the abundance and biomass of endolithic algae have not been directly assessed on ETP reefs, it seems logical to suggest that they most likely achieve high abundances as a result of the combination of low pH seawater, as well as high nutrients. The precipitation of carbonate cements is very low throughout the ETP and microborings were never infilled (Manzello et al. 2008), which is common in other shallow-water carbonate environments. Furthermore, the only limited cements that were observed were aragonitic; no high-mg calcite precipitates or cements were found. This follows the general scheme supporting an overriding thermodynamic control on cement precipitation given that high-mg calcite is more soluble than aragonite and is hypothesized to be a first responder to OA (Andersson et al. 2008). Certain organic coatings/matrices, or the creation of microenvironments due to biological activity, may ultimately be a localized driver of cementation in carbonate depositional environments, including coral reefs (e.g., Reid and Macintyre 1998), but the absence of significant cementation in ETP coral reefs suggests that seawater highly supersaturated with respect to aragonite is a prerequisite for these processes.

Bioerosion by clionaid sponges is also expected to increase in a high-CO_2 world (Wisshak et al. 2012; Fang et al. 2013, 2014; Enochs et al. 2015). Dissolution by the common Caribbean clionaid sponge *Pione lampa* (formerly *Cliona lampa*) is predicted to increase 99 % by the year 2100 due to OA, which is almost two times the anticipated depression in coral calcification (Enochs et al. 2015). Fang et al. (2013) showed that both sponge biomass and bioerosion rate increased in the zooxanthellate Pacific clionaid sponge *Cliona orientalis* with exposure to combined low pH and high temperature conditions. However, these workers found that under experimental conditions mimicking elevated temperatures and CO_2 concentration expected by the end of the century for a business-as-usual emissions scenario, *C. orientalis* bleached and *Symbiodinium* population abundances decreased with increasing CO_2. In spite of this, the bleached sponges under the highest CO_2 and temperature treatments had the greatest rates of bioerosion, even though sponge biomass declined with bleaching and was higher at lower CO_2 levels. In a related study, these workers found that *C. orientalis* consumed more carbon than it produced at high temperatures (Fang et al. 2014). As a result, the stimulation of bioerosion with ocean acidification in this species may be limited ultimately by high temperatures due to bleaching, reductions in biomass, and an overall negative energy balance (Fang et al. 2014). Zooxanthellate excavating sponges may display increased bioerosion rates with acidification to an upper thermal threshold, beyond which rates would likely decline due to bleaching, and cease, if mortality occurs. There could be an optimal pH as well where sponge dissolution peaks as rates of bioerosion decline at the highest CO_2 values for the azooxanthellate sponge *P. lampa* (Enochs et al. 2015).

18.4.3 Interacting Effects of Warming and Acidification

Historical and recent coral growth investigations have revealed the species-specific response of ETP corals to thermal stress and OA is complex. Two massive agariciid coral species (*Pavona clavus* and *Pavona gigantea*) have similar extension rates across natural CO_2 gradients, but are highly susceptible to thermal stress. Branching pocilloporid corals have demonstrated an increased tolerance to recurrent thermal stress events, potentially showing some ability to cope with warming (Glynn et al. 2001; Baker et al. 2004; however, see LaJeunesse et al. 2007, 2008). Pocilloporids have suffered a significant decline in growth rate at the Uva Island reef in Panama, however, possibly due to their increased temperature tolerance from hosting thermally resistant symbionts, OA, or both combined (Manzello 2010b). Despite their sensitivity to thermal stress, the massive pavonid corals rarely suffer complete, whole-colony mortality as tissues usually survive on the sides of the colony not exposed to direct sunlight (Glynn et al. 2001). In summary, the massive pavonids, like many other massive coral taxa, appear to be more tolerant to the combination of OA and ocean warming.

Recent work has shown that warming and acidification interact synergistically to impact corals. Anthony et al. (2008) demonstrated that both the massive coral *Porites lobata* and the branching coral *Acropora intermedia* were more susceptible to bleaching at elevated temperatures when subjected to low pH, compared to susceptibility in waters of contemporary pH levels for the Great Barrier Reef. In fact, they concluded that acidification has a greater impact on coral bleaching and productivity than on calcification. While experiments examining interactions between these factors are still at an early stage, it appears that the effects of warming and acidification may be exacerbated when both occur together. When rising temperatures remain below stressful levels, however, elevated thermal conditions may offset growth depression due to acidification (Lough and Barnes 2000; Cooper et al. 2012).

18.4.4 The Future of $CaCO_3$ Production on ETP Reefs

As stated earlier, ETP reefs provide a real-world example of coral reef growth and development in low-Ω_{arag} waters. This provides a unique opportunity to examine various aspects of $CaCO_3$ budgets under low-Ω_{arag} conditions in the present day. The precipitation of inorganic cements is highly limited in these low-Ω_{arag} reef environments. The thickness of ETP pocilloporid reef frameworks reflects Ω_{arag} in a positive, linear fashion (Fig. 18.4), illustrating the net result of coral calcification ($CaCO_3$ production) minus its loss (erosion) under high-pCO_2. These poorly cemented reef framework components are only held in place by a thin veneer of encrusting organisms, namely crustose coralline algae (CCA) and an organic matrix of sponges and other associated organisms. This point is important given that the geologic record suggests that encrustation by CCA is insignificant and subordinate to cementation in the construction and binding of framework structures (Macintyre 1997). Indeed, bioerosion rates in the Galápagos Islands and Panama are among the highest measured for any reef system to date (Glynn et al. 1979; Glynn 1988; Eakin 1996; Reaka-Kudla et al. 1996; see Chap. 12, Alvarado et al.).

Even with societal or governmental action to begin reducing emissions, in less than 40 years all of the ETP and most of the world's reefs could be at or below Ω_{arag} levels now seen in the Galápagos Islands (van Hooidonk et al. 2014). Without major changes in global fossil fuel use, corals will experience carbonate conditions similar to those of the last great extinction event during the Eocene by the end of this century (Zachos et al. 2005).

Coral reefs are declining globally and the present condition of Caribbean reefs may be the most alarming. There have been multiple interacting disturbances impacting Caribbean coral reefs that have directly caused, or acted to exacerbate large-scale coral mortality. The collapse of Caribbean coral reefs has been attributed to several factors that include: (1) white-band disease, which decimated the acroporid corals that were historically the dominant reef-builders in shallow environments, (2) the basin-wide ecological extinction of the keystone sea urchin herbivore *Diadema antillarum* due to an unidentified pathogen, (3) overfishing, (4) coral bleaching, and (5) land-based sources of pollution (Hughes 1994; Aronson and Precht 2001; Jackson et al. 2001; Eakin et al. 2010). Live coral cover has declined by about 80 % since the 1970s, the remaining reef frameworks are losing architectural complexity, the production of $CaCO_3$ has decreased to half of historical averages, and nearly one-third of sites recently surveyed were net erosional (Gardner et al. 2003; Alvarez-Filip et al. 2009; Perry et al. 2013). Many Caribbean reefs are in *accretionary stasis*, which means that they are at or close to $CaCO_3$ budget neutral; leading to concern about the persistence of architecturally complex reef framework structures (Perry et al. 2013).

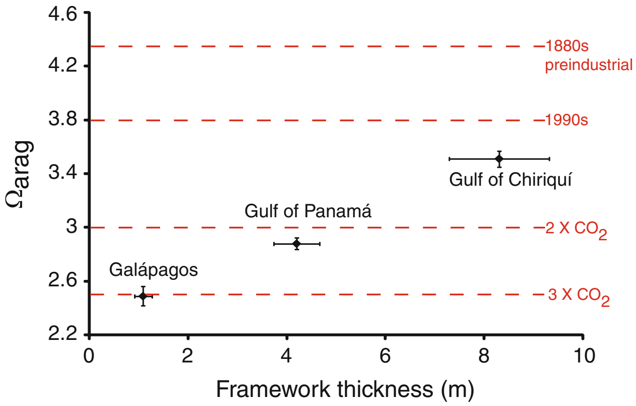

Fig. 18.4 Mean maximum coral reef framework thickness (m, ±SE) in eastern tropical Pacific relative to saturation state of aragonite, Ω_{arag}. Estimated values of Ω_{arag} for average tropical surface ocean as a function of differing levels of atmospheric CO_2 shown in red. From Manzello (2009)

Kennedy et al. (2013) simulated carbonate budget dynamics of Caribbean coral reefs based on the expected ecological response to the latest climate projections with the interacting role of local management of fisheries and land-based sources of pollution. A trend towards net erosion was apparent under all increased temperature and CO_2 scenarios, however, local-scale management of fisheries, specifically protection of parrotfishes, delayed the transition to reef loss by a decade. Positive $CaCO_3$ budgets were generated only when local management occurred in concert with aggressive emission reductions to limit global warming to less than 2 °C. Coral calcification declines from warming and acidification were most important in carbonate budget simulations for healthy, coral-dominated reefs. The controls on overall bioerosion rate (e.g., sea urchin population sizes, sponge boring rates, nutrification) became the dominant drivers of the carbonate budget with low coral cover.

Unlike anywhere else in the world, the ETP displays a continuum of thermal stress and CO_2 inputs up to levels at which reef building is terminated and reef structures are lost (Manzello 2009). A thermal anomaly of 2–3 °C for several months killed 95–97 % of zooxanthellate corals in the Galápagos Islands during the 1982–83 ENSO (Glynn 1990). Reef structures were completely lost in <10 years in this natural laboratory (Glynn 1994; Manzello 2009). The carbonate chemistry conditions in the Galápagos Islands provide an analog to what is expected for the rest of the tropical surface ocean with a doubling ($2 \times CO_2$: 560 ppm CO_2, $\Omega_{arag} = 3.0$) and tripling of atmospheric CO_2 ($3 \times CO_2$: 840 ppm CO_2, $\Omega_{arag} = 2.5$) (Manzello et al. 2008). Ω_{arag} values in the southern Galápagos Islands are commonly <3.0 and mean values at one site have been measured as low as 2.3 (Manzello 2010a; Manzello et al. 2014). Conversely, reef frameworks, while fragile, have persisted in Panamá despite net erosion following two severe ENSO events (Eakin 2001). Ω_{arag} values in Panama range from approximately 2.8 to 3.0 in the upwelling Gulf of Panama and from 3.0 to 3.5 in the non-upwelling Gulf of Chiriquí (Manzello 2010a). The thermal anomaly in Panama was 1–2 °C for two months during the 1982–83 ENSO (Podestá and Glynn 2001; see Chap. 8, Glynn et al.). More than 75 % of all zooxanthellate corals died in Panama (Glynn 1990), but sufficient numbers of the predominant reef builders survived, and recovery has been prolific despite another very strong ENSO event in 1997–98 (Glynn and Fong 2006). This suggests that the upper limit for reef growth and persistence may be a 2–3 °C thermal anomaly sustained in excess of two months during the warmest time of the year under more than a doubling of CO_2.

ENSO variability is expected to continue into the future and the frequency of extreme El Niño events is predicted to increase (Cai et al. 2014). The models do project substantial increases in extreme temperatures that include the length, frequency, and/or intensity of warm spells (IPCC 2011). As climate change raises the baseline temperatures upon which extreme events such as El Niño occur, even such events that were not severe in the past become severe in the future. Therefore, there is reason to expect more frequent and severe coral reef bleaching in the ETP in the coming years.

The existence of coral reefs beyond this century is in jeopardy. The concern over the dramatic losses of live coral (Gardner et al. 2003) has quickly evolved to a fear that the underlying framework of coral reefs may erode away in a high-CO_2 world (Hoegh-Guldberg et al. 2007; Manzello et al. 2008; Perry et al. 2013). Coral cover has declined across large geographic scales (Gardner et al. 2003; De'ath et al. 2012), leading to concomitant declines in $CaCO_3$ production. Furthermore, declines in coral growth and calcification have been documented in all tropical seas over the past 30 years (Edmunds 2007; Cooper et al. 2008; Bak et al. 2009; De'ath et al. 2009; Tanzil et al. 2009; Manzello 2010b). The production of $CaCO_3$ on coral reefs has likely declined at a global scale. As a result, the future impacts of OA to the negative side of the coral reef carbonate budget, via stimulation of biologically-mediated dissolution (bioerosion), may be more detrimental than the decline of coral calcification. Indeed, Kennedy et al. (2013) explicitly demonstrated that changes to coral calcification are most significant to the $CaCO_3$ budget when coral cover is high. When coral cover is low, bioerosion becomes the dominant process.

In the ETP, the combination of natural ocean acidification and extreme temperatures during El Niño events has led to the development of fragile, uncemented reefs with a great susceptibility to major losses from thermal stress events. Unfortunately, global ocean acidification and warming will threaten many reefs worldwide with similar conditions within this century and the current trajectories of fossil fuel use will soon drive Ω_{arag} levels in the ETP much lower than those surrounding any coral reefs extant today. At the same time, continued warming threatens the return of mass coral bleaching. Today, coral reefs of the ETP can serve as a model for reef conditions we will likely witness in other regions within a few decades.

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