Holocene Reef Development in the Eastern Tropical Pacific

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Abstract

Contrary to early assessments, the eastern tropical Pacific (ETP) is not devoid of well-developed reefs. Significant accumulations of Holocene reef framework are present throughout the region, although they tend to be poorly consolidated, lack the submarine cementation common on most reefs elsewhere in the world, and are subject to considerable bioerosion. These reef frameworks began accreting as early as 7000 years ago. The thickest accumulations of *Pocillopora* frameworks occur in coastal areas of Mexico, Costa Rica, Panama, and Colombia, but reefs composed of massive corals—species of *Porites*, *Pavona*, or *Gardineroseris*—are present throughout the region. Reef development in the ETP is limited by a variety of characteristics of the physical environment. Because of high turbidity in most areas, reef development is generally restricted to less than ~10 m depth. The spatial extent of reefs in the ETP is also limited from the combined influences of wave action and upwelling. Most reefs in the ETP are only a few hectares in size and the best-developed reefs generally occur in areas sheltered from strong oceanic influence. Upwelling also influences long-term trends in reef development in the region. There does not appear to be a significant impact of upwelling on the millennial-scale growth rates of Panamanian reefs; however, reefs in upwelling environments typically have thinner frameworks than nearby reefs in non-upwelling environments. Furthermore, upwelling may have contributed to a historic shutdown of reef development in Costa Rica and Panama. Although both ecological and oceanographic disturbances have had some impact on the long-term development of reefs in the ETP, the most important control on reef development in this region throughout the Holocene has most likely been the El Niño–Southern Oscillation (ENSO). ENSO activity—especially that of the 1982–83 and 1997–98 El Niño events—has shaped the landscape of coral reefs across the ETP both in recent decades and

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in the past. Reefs in Pacific Panama and Costa Rica experienced a 2500-year hiatus in vertical growth beginning ~4100 years ago as a result of enhanced ENSO activity. Although the degree of framework accumulation and rate of reef accretion in some parts of the ETP are more similar to that of the western Atlantic than previously thought, the region still remains a marginal environment for reef development. Given the dominant role that climatic variability has played in controlling reef development in the past, the future of reefs in the ETP under accelerating climate change remains uncertain.

Keywords

Reef accretion • Paleoecology • Upwelling • El Niño–Southern Oscillation • Latin American reefs

6.1 Introduction

This chapter reviews the known records of Holocene coral-reef development across the eastern tropical Pacific (ETP), including the reefs of Mexico, Nicaragua, Costa Rica, Panama, Colombia, Ecuador, Clipperton Atoll, and Easter Island (Rapa Nui). Although initial reports suggested a lack of coral-reef development in the ETP (e.g., Darwin 1874), later studies identified some reef formations with rapid accumulation rates that initiated up to 7000 years ago (e.g., Toth 2013; Hendrickson 2014). These reefs exhibit considerable variation in areal extent, degree of framework construction, and depth of formation (Glynn 2000; Cortés 2011). Although we identify a variety of geological and ecological characteristics common to most reefs in the region, considerable variety exists in the Holocene histories of coral reefs of the ETP. We discuss these variations as they relate to geography, environmental changes, and physical conditions, including temperature, turbidity, shelf area, and antecedent topography. By synthesizing the known records of reef development, we evaluate the proposition that reef development is generally poor in the ETP. Finally, we discuss the prospects for reef development over the next decades to centuries under conditions of accelerating climate change.

6.2 Regional Characteristics of Eastern Pacific Coral Reefs

6.2.1 Ecology and Structure

Coral reefs in the ETP are predominantly formed by interlocking colonies of the branching coral *Pocillopora damicornis* and/or near-monogeneric stands of massive corals of the genera *Porites*, *Pavona*, or *Gardineroseris* (Glynn 1976; Guzmán and Cortés 1989a; Macintyre et al. 1992; Cortés 1997; Glynn and Maté 1997; Glynn and Ault 2000). Fringing, *Pocillopora*-dominated reefs are common in the sheltered embayments of offshore islands in the ETP, but they can also be found along the mainland coast. Most of the well-developed reefs throughout the eastern Pacific share a typical zonation pattern. The shallow zone is generally dominated by *Pocillopora* spp., and massive species increase in dominance with depth. On the reef flat, which is the shallowest part of the reef, coral cover is patchy. Living coral cover is generally highest at the seaward edge along the upper reef slope, where *Pocillopora* growth rates are high. This upper reef slope typically has the thickest accumulation of Holocene framework. For example, a cross-reef transect of drill-cores collected from a fringing reef in the Secas Islands, Gulf of Chiriquí, Panama penetrated 2.8 m on the reef flat, 8.2 and 12.0 m on the reef slope, and only 1.2 m at the base of the fore reef (Glynn and Macintyre 1977). Although coral diversity increases in the deeper reef zones, coral cover declines with depth and carbonate accumulation is minimal in the deepest zones (Glynn 1976).

6.2.2 Deposition, Bioerosion, and the Fossil Record

Coral reefs of the ETP typically grow in relatively low-energy environments, and because the saturation state of aragonite is low in the region the reefs show little evidence of the type of submarine lithification that is common in coral reefs of the western Atlantic (Macintyre and Glynn 1976; Glynn and Macintyre 1977; Cortés 1997; Manzello et al. 2008). Likewise, coralline algae, although present in the ETP, do not generally consolidate reef structures to the extent they do elsewhere (Glynn and Maté 1997). Reef frameworks of the ETP are stabilized primarily by interdigitation of the *Pocillopora* branches and by the fine sediments the branches entrain, rather than by cementation. As a result, slumping of small patches of over-steepened framework is common on reef slopes in the ETP (Glynn 1976). The lack of cementation also makes these reefs highly susceptible to the destructive forces of storms and wave action; therefore, reefs that have a record of Holocene accumulation are typically located in sheltered embayments (Dana 1975; Glynn and Ault 2000).

Framework accumulation is also limited by the negative influence of bioerosion (Glynn 1997). Bioerosion is common on all reefs of the ETP, although the relative importance of internal bioeroders (primarily clionid sponges and lithophagine bivalves) and external grazers (primarily echinoids) differs from region to region (Cortés 1997; see Chap. 12, Alvarado et al.). In the Galápagos, bioerosion by the sea urchin *Eucidaris galapagensis* can reduce net accumulation by up to 20 %, even where coral cover is high (Glynn et al. 1979), but the impacts of bioerosion on reef accretion are even more severe following major disturbance events (Glynn 1988, 1997; Eakin 1992, 1996; Cortés 1997; Fonseca et al. 2006).

The 1982–83 El Niño–Southern Oscillation (ENSO) event killed 52–97 % of living coral in the ETP (Glynn et al. 1988, 2001). The associated increase in echinoid activity in the Galápagos, Costa Rica, and Pacific Panama, led to rates of bioerosion that exceeded rates of reef-framework growth (Glynn 1988; Eakin 1992, 1996; Reaka-Kudla et al. 1996; Glynn and Wellington 2007; see Chap. 12, Alvarado et al.). A similar increase in bioerosion was observed on Mexican reefs after the 1987 El Niño (Glynn and Leyte-Morales 1997). Most reefs have since recovered their coral populations, but much of the framework that existed in the Galápagos prior to 1982–83 has been eliminated by bioerosion (Macintyre et al. 1992; Glynn et al. 2001, 2015; Glynn 2003). It is unlikely that bioerosion can disrupt the preservation of coral skeletons once they are buried and stabilized by fine sediment, but bioerosion is clearly important in determining the completeness of the fossil record in the ETP.

6.3 Initiation of Holocene Reef Development

The sea-level history in the eastern Pacific over the last 10,000 years (Curray et al. 1969; Hopley 1982) is generally thought to be similar to that reported for the western Atlantic (e.g., Lighty et al. 1982; Toscano and Macintyre 2003), although a comprehensive sea-level curve has not yet been generated for the region. If the Caribbean sea-level model is applicable, then coral reefs on the continental and insular shelves in the ETP could have become established at least 7000 year BP (Toscano and Macintyre 2003; Toth 2013). In general, it appears that reefs first began to grow in regions of the ETP that are relatively sheltered from oceanic influences (Macintyre et al. 1992). Reef development in more exposed areas did not begin until recent millennia (Cortés 1993).

One of the earliest dates for reef initiation in the region comes from a push-core we extracted from a reef in the Gulf of Panama. Our core EP09-28, from the reef at Playa Larga, off Contadora Island in the Pearl Islands Archipelago (8°37′ N, 79°01′W; Fig. 6.1), penetrated 442 cm to bedrock. A sample of *Pocillopora damicornis* from the base of the core yielded a calibrated radiocarbon date of 6956 cal year BP (calibrated calendar years before 1950; 2-sigma range [95 % confidence interval] 7094–6645 cal year BP), giving a date of reef initiation consistent with the inferred time of shelf-flooding. [Dates from the Gulf of Panama were calibrated using local reservoir corrections that we established (Toth et al. 2012, 2015; Toth 2013). Dates from other locations were calibrated using the global marine reservoir correction because no historical reservoir corrections are available for other parts of the ETP. Dates from Macintyre et al. (1992); Cortés et al. (1994) were also corrected for isotopic fractionation using the assumed value of 0 ± 4.]

Most published reports suggest that significant reef development in the ETP began between 5600 and 4500 cal year BP, when sea level presumably neared its present elevation (Dana 1975; Glynn and Macintyre 1977; Cortés et al. 1994). Another core we collected, EP09-32 from the nearby Saboga Island reef, is more consistent with this conclusion. EP09-32 penetrated 363 cm to bedrock. The recovery was 228 cm, of which the bottom 43 cm consisted of sand and fragments of coralline algae with no coral. The earliest date of active reef growth from this core, determined from the radiocarbon date of a sample of *Pocillopora* directly above the layer of sand and coralline algae, was 4348 cal year BP (2-sigma range 4558–4131 cal year BP). Similar lag times between shelf-flooding and reef initiation have been reported for other geographic regions (Hopley et al. 1978; Davies et al. 1985; Macintyre et al. 1985; Montaggioni 1988). The lags between flooding and reef-framework construction were likely caused by extensive erosion of the soil and sediment cover on the adjacent shorelines, which created conditions hostile to coral settlement and growth.

Finally, many coral reefs in the eastern Pacific exist as incipient structures, which, despite exhibiting significant vertical accumulation, were only established within the last 1000 years. They include reefs composed of massive corals, such as those off Caño and Cocos Islands in Costa Rica (Macintyre et al. 1992), as well as seemingly complex fringing *Pocillopora* reefs off many of the islands of Panama and the Galápagos. For example, the framework of the *Pocillopora*-dominated reef of Mogo Mogo Island in the Pearl Islands is only 50 cm thick and established within the past 50 years.

Our cores suggest that the well-developed reefs in Pacific Panama were dominated by coralline algae in their earliest stages of development. Soon after, the free-living coral *Psammocora* was dominant for a short period before the

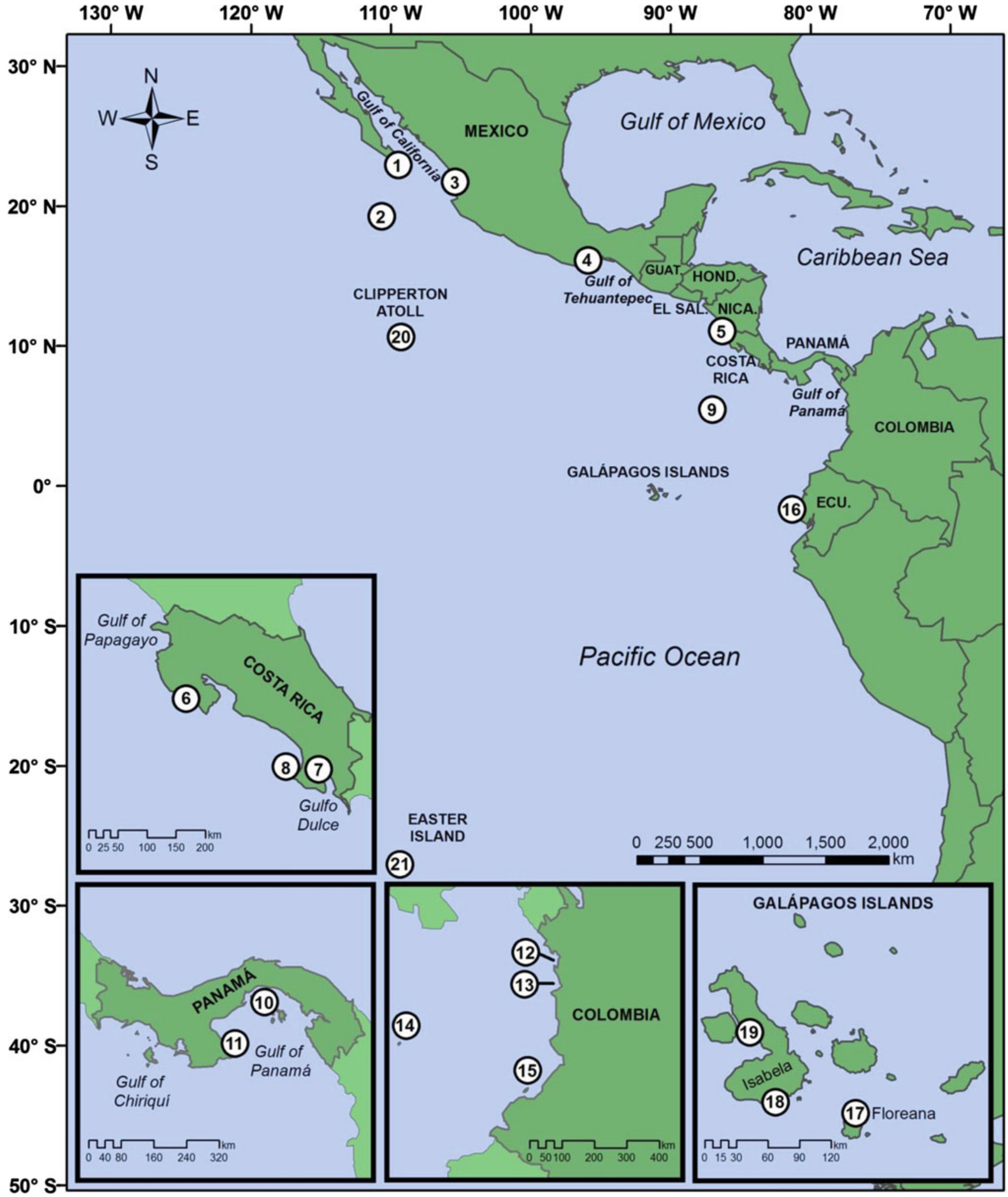

Fig. 6.1 Index map showing location of selected eastern Pacific reefs from Mexico to Ecuador. Numbered sites indicate the locations of reefs discussed in text: (1) Cabo Pulmo, (2) Revillagigedo Archipelago, (3) Nayarit, (4) Huatulco, (5) San Juan del Sur, (6) Sámara, (7) Punta Islotes, (8) Caño Island, (9) Cocos Island, (10) Pearl Islands Archipelago, (11) Iguana Island, (12) Gulf of Cupica, (13) Ensenada de Utría, (14) Malpelo Island, (15) Gorgona Island, (16) Sucre and La Plata Islands, (17) Champion, Onslow, and Floreana Island coral reefs, (18) Villamil coral reef, (19) Urvina Bay, (20) Clipperton Atoll, and (21) Easter Island (Rapa Nui)

Pocillopora-dominated assemblages typical of modern reefs were established. This pattern of reef development is similar to that observed in the uplifted reef section at Urvina Bay, Galápagos (Colgan and Malmquist 1987), and in extant reefs in Costa Rica (Bezy et al. 2006). It is possible, therefore, that a primary successional sequence from coralline algae, to free-living corals like *Psammocora,* to dominance by *Pocillopora* is common to many reefs in the ETP.

6.4 Documented Records of Reef-Framework Construction in the Eastern Pacific

6.4.1 Mexico

Early reports from Pacific Mexico suggested that coral-reef development in this region was minimal (Reyes-Bonilla 2003). Although many Mexican reefs exist only as veneers on the antecedent substrate, further exploration of the region in recent decades has revealed a number of substantial reef formations (Reyes-Bonilla 1992, 1993a, b, 2003; Carriquiry and Reyes-Bonilla 1997; Glynn and Leyte-Morales 1997; Pérez-Vivar et al. 2006), some of which may rival the best-developed coral reefs in the ETP (Glynn and Leyte-Morales 1997). In addition to Holocene reef deposition, some areas of the Mexican Pacific appear to contain continuous fossil records extending back to the Pliocene epoch (Reyes-Bonilla 1992; see Chap. 2, López-Pérez). The coral reefs of Pacific Mexico can be divided into three biogeographic subunits, following Reyes-Bonilla (2003): the Gulf of California, the Revillagigedo Archipelago, and the tropical (coastal) Mexican Pacific.

6.4.1.1 Gulf of California

The Gulf of California contains some of the best-studied reefs in the Mexican Pacific (Reyes-Bonilla 2003). True reef development is limited in this northernmost region of the ETP, but significant reef structures exist in some parts of the gulf (Reyes-Bonilla 1993b, 2003). The largest of these is the reef at Cabo Pulmo (23°20′N, 109°25′W; Fig. 6.1), near the southern tip of the Baja California Peninsula (Reyes-Bonilla 1993a, b, 2003). Although the Cabo Pulmo reef is considered to be the northernmost coral reef in the ETP, there is little retention of carbonate framework; therefore, in many ways it is atypical of coral reefs in other geographic regions (Riegl et al. 2007). Like most coral reefs in the ETP, the 15-ha reef at Cabo Pulmo is dominated by *Pocillopora* spp. (Reyes-Bonilla 1993b), but massive *Porites* and *Pavona* spp. increase in abundance below 6 m depth (Reyes-Bonilla 2003; Carriquiry and Villaescusa 2010). Unlike most areas of the ETP, however, the reef at Cabo Pulmo has been reported as being 'well-cemented' (Carriquiry and Villaescusa 2010), which is surprising considering the low aragonite saturation state at this northerly latitude and the putatively low cementation of the ETP as a whole (Kleypas et al. 1999b; Manzello et al. 2008). The maximum Holocene framework accumulation at Cabo Pulmo was approximately 3 m (Table 6.1; Reyes-Bonilla 2003; Carriquiry and Villaescusa 2010).

6.4.1.2 Revillagigedo Archipelago

The oceanic Revillagigedo Archipelago is located approximately 700 km southwest of the Gulf of California (Fig. 6.1) and includes the islands of Socorro, Clarión, and San Benedicto, and the rock pinnacle Roca Partida (see also Fig. 5.8 in Chap. 5, Glynn et al.). The best-developed reefs in the archipelago are the *Pocillopora*-dominanted fringing reefs that occur along the coasts of Socorro and Clarión Islands (18°20′N, 114°43′W and 18°48′N, 110°57′W, respectively; Reyes-Bonilla 2003), although neither is more than a hectare in area (Ketchum and Reyes-Bonilla 1997). Despite the small size of the reefs, the archipelago contains the greatest number of coral species in the Mexican Pacific (Reyes-Bonilla 2003). Holocene carbonate accumulation in the Revillagigedo Archipelago is similar to that in the Gulf of California, with reef frameworks reaching 3 m in thickness at Clarión Island and 2 m at Socorro Island (Table 6.1; Reyes-Bonilla 2003).

6.4.1.3 Tropical Mexican Pacific

The southernmost region of Pacific Mexico, the tropical Mexican Pacific, extends from 21° to 15°N along the Mexican coastline (Reyes-Bonilla 2003). Much of the coastline is dominated by sandy substrates that do not support reef development, so although isolated patches of coral can be found throughout the region, true coral reefs are confined to the coasts of the states of Nayarit and Oaxaca (Reyes-Bonilla 1993b, 2003).

Small, fringing *Pocillopora* reefs are common around the islands near the southern coasts of Nayarit (20–21°N; Carriquiry and Reyes-Bonilla 1997; Reyes-Bonilla 2003). The reefs at Careyeros, Corral del Risco, and Punta Mita Islands exhibit only 1–3 m of Holocene framework accumulation, likely due to the narrowness of the coastal shelves (Table 6.1; Carriquiry and Reyes-Bonilla 1997). The best-developed reefs are found at nearby Jaltemba Island, where thicker framework accumulation has been reported (Reyes-Bonilla 2003). Unlike the nearshore islands of Nayarit, the oceanic Marías Islands to the west of mainland Nayarit reveal only superficial reef development (Pérez-Vivar et al. 2006).

The southernmost reefs in the Mexican Pacific are located along the southern coast of Oaxaca (15°N), between Puerto Ángel and Huatulco (Reyes-Bonilla 1993b). This region of Mexico includes the Gulf of Tehuantepec, the northernmost of three major upwelling centers along the Central American

Table 6.1 Maximum estimates of Holocene reef accumulation and the dominant coral genera on the ETP reefs described in this chapter

Location	Dominant Genus	Maximum thickness	Reference
Mexico			
Cabo Pulmo, Gulf of California	*Pocillopora*	3 m[u]	Reyes-Bonilla (2003)
Revillagigedo Archipelago	*Pocillopora*	3 m[u]	Reyes-Bonilla (2003)
Nayarit, Tropical Mexican Pacific	*Pocillopora*	3 m[u]	Carriquiry and Reyes-Bonilla (1997)
Huatulco, Tropical Mexican Pacific	*Pocillopora*	6 m[v]	Glynn and Leyte-Morales (1997)
Costa Rica			
Culebra Bay, Gulf of Papagayo	*Pocillopora*	3 m[p]	Glynn et al. (1983)
Punta Islotes, Golfo Dulce	*Pocillopora*	9 m[c]	Cortés et al. (1994)
Los Mogos, Golfo Dulce	*Porites*	11 m[v]	Glynn et al. (1983)
Caño Island	*Pocillopora*	2.4 m[p]	Guzmán (1986)
Cocos Island	*Porites*	3.1 m[c]	Macintyre et al. (1992)
Panama			
Gulf of Chiriquí			
Secas Island	*Pocillopora*	13.4 m[p]	Glynn and Macintyre (1977)
Uva Island	*Pocillopora*	11 m[c]	Glynn and Macintyre (1977)
Gulf of Panama			
Saboga Island	*Pocillopora*	5.6 m[c]	Glynn and Macintyre (1977)
Contadora Island	*Pocillopora*	4.6 m[p]	Glynn and Macintyre (1977)
Iguana Island	*Pocillopora*	6.1 m[p]	Glynn and Macintyre (1977)
Colombia			
Tebada Island, Gulf of Cupica	*Pocillopora*	4 m[u]	Zapata and Vargas-Ángel (2003)
La Chola, Ensenada de Utría	*Pocillopora*	4 m[p,c]	Vargas-Ángel (2001)
La Azufrada, Gorgona Island	*Pocillopora*	8 m[p]	Glynn et al. (1982)
Ecuador			
La Plata Island	*Pavona*	6 m[v]	Glynn and Wellington (1983)
Isabela Island, Galápagos	*Pocillopora*	4 m[v]	Glynn and Wellington (1983)
Bartolomé Island, Galápagos	*Porites*	5 m[v]	Glynn and Wellington (1983)
Champion Island, Galápagos	*Pavona*	5 m[v]	Glynn (2003)
Onslow Island, Galápagos	*Psammocora*	1.5 m[c]	Feingold (1995)
Clipperton Atoll	*Pocillopora*	6 m[v]	Carricart-Ganivet and Reyes-Bonilla (1999)
Easter Island (Rapa Nui)	*Porites*	10 m[v]	Hubbard and Garcia (2003), Glynn et al. (2007)

Superscripts indicate basis of estimates:
[c] Coring
[p] Probing
[v] Visual estimation based on reef topography
[u] Unknown

coast (the others being the Gulf of Papagayo in Nicaragua/Costa Rica, and the Gulf of Panama; Fig. 6.1; Glynn and Leyte-Morales 1997). These reefs are dominated by *Pocillopora* spp. and, like the reefs in the Gulf of Panama, are generally found in small, sheltered embayments. Despite the putative limitation of reef development due to upwelling, coral reefs in this region have attained Holocene framework accumulations comparable to those in other regions of the ETP. The framework thickness of most reefs is between 3 and 4 m, but Holocene framework accumulations of up to 6 m have been recorded (Table 6.1; Glynn and Leyte-Morales 1997), comparable to Holocene framework accumulation in the Gulf of Panama (Glynn and Macintyre 1977).

6.4.2 Guatemala, El Salvador, and Honduras

Few, if any, true coral reefs occur between Mexico and Nicaragua, although there is likely some connectivity between the regions (Glynn and Ault 2000; see Chap. 5, Glynn et al., and Chap. 16, Lessios and Baums). This 'Central American faunal gap' may be related to the limited amount of hard substrate available for larval settlement along the coasts of Guatemala, El Salvador, and Honduras. Isolated coral assemblages have been found in some areas such as Los Cóbanos, El Salvador (13°32′N, 89°48′W), but there does not appear to be any significant framework accumulation in this region (Reyes-Bonilla and Barraza 2003).

6.4.3 Nicaragua

Recent surveys at San Juan del Sur, Nicaragua (11°15′N, 85°52′W; Fig. 6.1) suggest that coral assemblages may be more abundant in this area than previously assumed. The dominant coral in this region is *Pavona gigantea*, but pocilloporids are also found in isolated patches (Alvarado et al. 2010, 2011). Coral cover is less than 10 % on average but approaches 20 % at Guacalito (11°22′N, 86°1′W) and Punta Gigante (11°23′N, 86°2′W). These northernmost sites at San Juan del Sur are least affected by seasonal upwelling in the nearby Gulf of Papagayo and appear to have the best development of coral assemblages in the region (Alvarado et al. 2011). It is unclear from Alvarado (2010, 2011) and colleagues' recent reports whether the coral assemblages of San Juan del Sur represent true coral reefs or incipient reef communities; there is, as yet, no information on the degree of carbonate accumulation in this region. Compared with other parts of the ETP, the coral assemblages of Nicaragua and other regions within the Central American faunal gap have been understudied. Perhaps with increased focus on these areas in the future, the faunal gap will be narrowed as more coral assemblages, and possibly even developed coral reefs, are discovered.

6.4.4 Costa Rica

Coral reefs are common along the Pacific coast of Costa Rica, from Santa Elena in the northwest to Golfo Dulce in the east near the Panamanian border. They also are found around the offshore islands of Cocos and Caño (Cortés and Jiménez 2003). As in southern Mexico, reefs in Costa Rica are most common in sheltered embayments where they are protected from wave stress (Glynn et al. 1983). Although the reefs of this region are generally less developed than those of Pacific Panama, considerable framework accumulation has been observed in some areas, including the Gulf of Papagayo, Golfo Dulce, and at Cocos and Caño Islands.

6.4.4.1 Gulf of Papagayo

In the Gulf of Papagayo, which is located in the northwestern region of Costa Rica (10°43′N, 85°48′W; Fig. 6.1), coral reefs are subject to strong seasonal upwelling. The upwelling season in Costa Rica is more protracted and produces lower water temperatures than in the Gulfs of Panama or Tehuantepec (Glynn et al. 1983; Alexander et al. 2012). As a result, the depth-range of the coral reefs is restricted: reef-building corals are abundant to only 5 m depth in the Gulf of Papagayo, compared with 15 m in nearby Golfo Dulce where there is no upwelling (Glynn et al. 1983). Additionally, massive corals in the Gulf of Papagayo have more boreholes and skeletal disconformities than massive corals in non-upwelling areas of Costa Rica and Panama. The numbers of boreholes and skeletal disconformities in the Gulf of Papagayo are also elevated relative to the Gulf of Panama, where there is upwelling (Glynn et al. 1983), supporting the contention that upwelling is more severe in Papagayo (cf. Highsmith 1980). Although upwelling generally slows coral growth in the ETP (Glynn 1977; Glynn et al. 1983), Jiménez and Cortés (2003) found that growth rates of *Pocillopora* spp., *Pavona clavus*, and *Psammocora stellata* were greater in the Gulf of Papagayo than in any other part of the ETP. They suggested that high nutrient levels during upwelling could be responsible for the elevated growth rates in this region (Jiménez and Cortés 2003), and that the effects of increased nutrient availability may override the negative impacts of low sea temperatures. The overall impacts of upwelling on coral reef development may, therefore, be more complex than originally recognized (Chollett et al. 2010).

In a geographic survey, Glynn et al. (1983) found that whereas most reefs in the southern part of Costa Rica were actively accreting, nearly all the reefs in the Papagayo region were dead. The dead reefs appeared to have been formed primarily by interlocking colonies of *Pocillopora damicornis*, which, at the time of the survey were covered by crustose coralline algae and algal turfs. The timing of reef degradation was determined by dating coral samples from dead reefs in the Gulf of Papagayo and Sámara Beach (9°51′N, 85°52′W; Fig. 6.1), located south of the gulf. Nine radiocarbon dates placed the timing of reef demise between 292 and 154 cal year BP, or 1660–1795 C.E. The apparent agreement between these dates and the timing of the Little Ice Age (LIA), a period of climatic cooling between about 1600 and 1900 C.E., led Glynn et al. (1983) to postulate that the LIA was the cause of coral mortality and reef degradation.

The LIA was a climatic phenomenon associated with centennial-scale southerly displacement of the Inter-Tropical Convergence Zone (ITCZ; Haug et al. 2001; Sachs et al.

2009). The ITCZ is the major driver of interannual variability in the ETP, and its annual southward migration during the boreal winter leads to intensification of the trade winds and the upwelling season in the Gulf of Papagayo and the other upwelling centers in the region (Poveda et al. 2006). Glynn et al. (1983) suggested that a more southerly position of the ITCZ during the LIA could have led to either more intense or more protracted upwelling seasons in the Gulf of Papagayo and Sámara, which may have overwhelmed the capacity of corals to survive. Analysis of $\delta^{18}O$ from the tips of dead coral colonies suggested that the corals died during an extreme low-temperature event, supporting their hypothesis (Glynn et al. 1983).

Reef probing by Glynn et al. (1983) suggested that the maximum Holocene framework accumulation in the Gulf of Papagayo is about 3 m (Table 6.1), which is significantly less than in the non-upwelling Golfo Dulce (discussed below). They concluded that coral reefs in the Gulf of Papagayo are significantly younger than those in the non-upwelling regions of Pacific Costa Rica. Using average coral growth rates from Pacific Panama, they estimated that the l-m-thick reef at Punta Gorda formed at about 800 year BP and the 2.2-m-thick reef at Santa Elena formed about 1700 year BP (Glynn et al. 1983). These could be conservative estimates (i.e., the reefs are probably older) because the actual coral growth rates in the Gulf of Papagayo are limited by seasonal upwelling.

6.4.4.2 Golfo Dulce

The Punta Islotes fringing reef is located in the innermost part of Golfo Dulce, about 50 km from the open ocean (8°28′N, 83°12′ W; Fig. 6.1). Living coral cover is less than 2 %, and most of the reef surface is covered by a filamentous algal mat (Fig. 6.2). During a paleoecological study in the late 1980s, nine core holes were drilled along four short transects on the reef (Fig. 6.3) and four vibracores were collected from the fore-reef talus slope (Cortés 1990a; Macintyre et al. 1992; Cortés et al. 1994). The cores ranged in penetration depth from 2.5–9 m (Table 6.1; Cortés et al. 1994), providing a minimum estimate of Holocene accumulation for this reef. Visual inspection of nearby Los Mogos reef suggested that *Porites*-framework accumulation at that site was ~11 m above the seafloor, which is the thickest massive-coral framework recorded in the ETP (Table 6.1; Glynn et al. 1983).

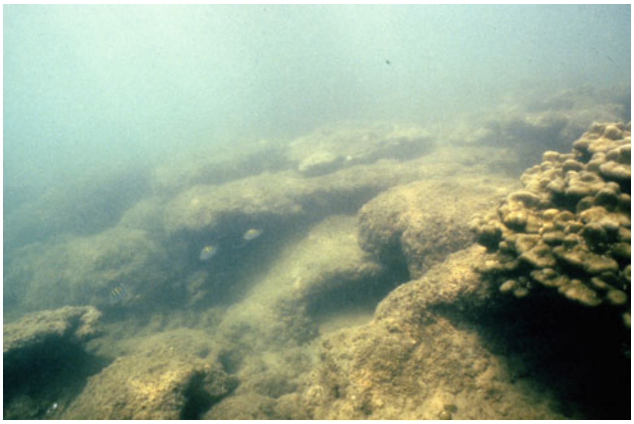

Fig. 6.2 Punta Islotes reef, Golfo Dulce, Costa Rica, 4 m depth, February 1989. Most of the large overlapping *Porites lobata* colonies are dead and covered with filamentous algae and sediments

Twenty-five radiocarbon dates from Punta Islotes reef, plotted in relation to the sea-level curve (Curray et al. 1969; Hopley 1982), led to the conclusion that the Cretaceous basaltic bench underlying the reef was flooded at least 6000 years ago. Coral debris from the fore-reef talus slope yielded a date of 6162 cal year BP (2-sigma range 6374–5928; Table 6.2), indicating a fairly short lag-time before the establishment of this reef. There is no record of significant reef development during the intervening 3000 years, and accretion rates during this period were only 0.9–1.5 m/1000 year. A secondary reef framework of *Porites lobata*, *P. damicornis*, and *Psammocora stellata* was established on the basaltic base about 2500 year BP and flourished for the next 2000 years. Average accretion rates over this period were 2.4 m/1000 year (Toth et al. 2012); however, during its most rapid stage of development from 1500–500 year BP, the reef at Punta Islotes accreted at a rate of 8.3 m/1000 year, which is comparable to centennial-scale accretion rates in the non-upwelling Gulf of Chiriquí, Panama, discussed below (Glynn and Macintyre 1977; Cortés et al. 1994). An increase in the outflow of nearby rivers caused a deterioration of water quality about 500 years ago. In recent times, deforestation on the adjacent shore resulted in increased sedimentation on the reef, which finally led to its modern, algal-covered state (Cortés et al. 1994).

6.4.4.3 Caño Island

This 3-km^2 island is located 15 km off the coast of Costa Rica (8°42′N, 83°52′W; Fig. 6.1; Guzmán and Cortés 1989a). Most of the reef-flat area currently consists of dead *Pocillopora damicornis* covered by crustose coralline algae, although a few living colonies of *P. damicornis, Pocillopora elegans*, and *Psammocora stellata* can also be found (Guzmán and Cortés 1989a). Probing of the dead *Pocillopora* framework showed that the maximum framework accumulation at Caño Island is about 2.4 m (Table 6.1; Guzmán 1986). The age of the *Pocillopora* reef at Caño Island is unknown.

Microatolls formed by colonies of *Porites lobata* (Fig. 6.4a) cover about 12 % of a 4.2-ha reef flat off the northern end of the island. Seaward of this reef flat are living and dead colonies of *Porites lobata*, on and between buttresses of metasedimentary rock (Guzmán and Cortés 1989a;

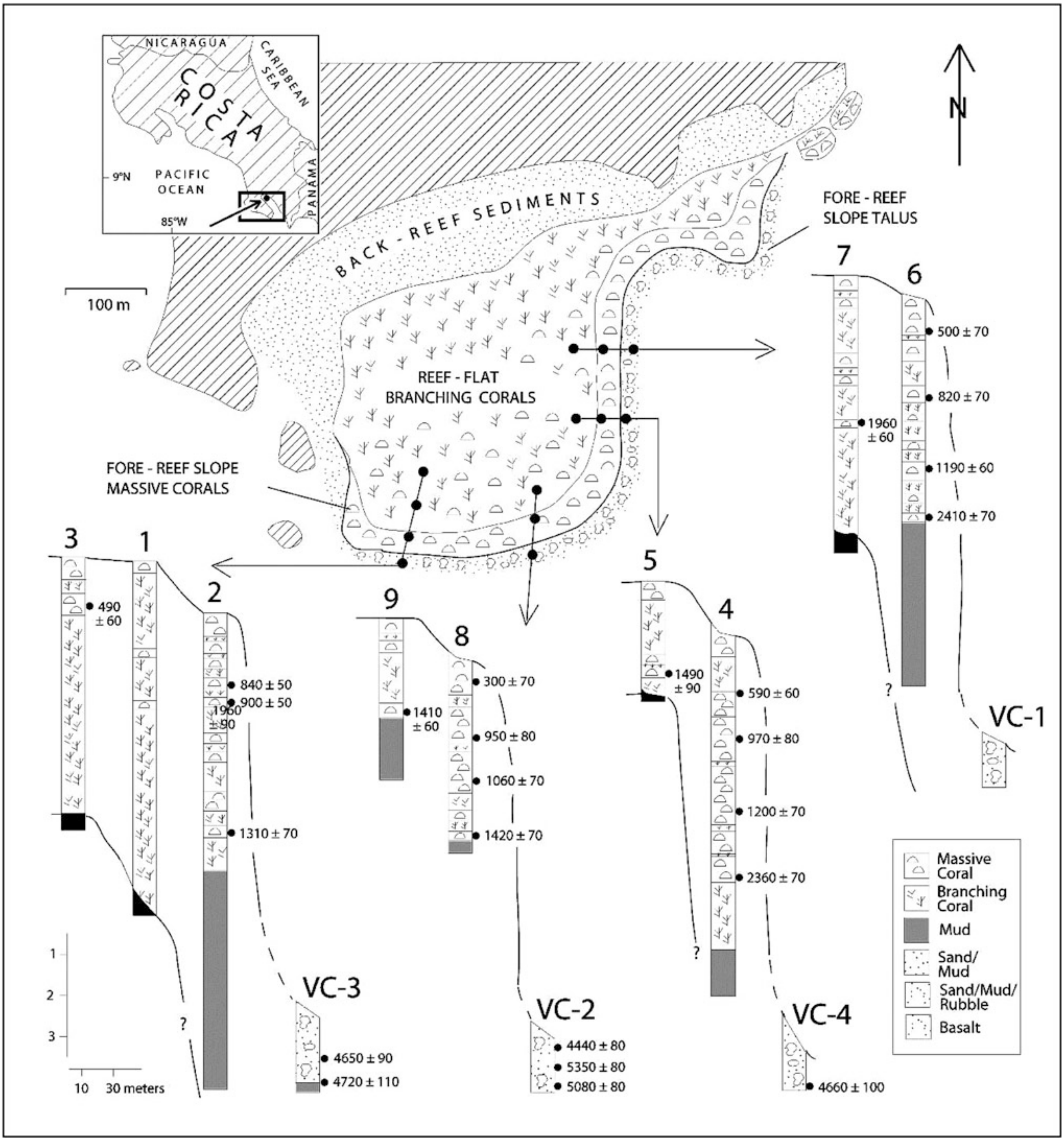

Fig. 6.3 Surface zonation and locations of nine reef cores and four vibracores on the talus slope of Punta Islotes reef. Core logs show the locations of 25 radiocarbon dates (from Cortés et al. 1994)

Macintyre et al. 1992). The buttresses mostly have a thin cover of crustose coralline algae and filamentous algal turf (Fig. 6.4b). Varieties of other corals are found on the reef slope; however, 95 % of the coral in this area was killed during the 1982–83 El Niño warming event (Cortés et al. 1984; Guzmán et al. 1987).

Five microatolls were overturned during a study by Macintyre et al. (1992) and the centers of initial growth at their bases were sampled and dated, yielding an average date of 279 cal year BP (2-sigma range 460–1 cal year BP). The base of a large overturned *Porites lobata* colony on the slope gave a date of 471 cal year BP (2-sigma range 610–

Table 6.2 Earliest records of Holocene reef initiation in the ETP

Location	Reef initiation	Reference
Clipperton Atoll	~5000 year BP	Carricart-Ganivet and Reyes-Bonilla (1999)
Costa Rica		
Punta Islotes, Golfo Dulce	6162 cal year BP	Cortés et al. (1994) (calibrated)
Panama		
Uva Island, Gulf of Chiriquí	5960 cal year BP	Glynn and Macintyre (1977) (calibrated)
Saboga Island, Gulf of Panama	4551 cal year BP	Toth (2013)
Contadora Island, Gulf of Panama	6907 cal year BP	Toth (2013)
Iguana Island, Gulf of Panama	6883 cal year BP	Toth (2013)
Ensenada de Utría, Colombia	3000 cal year	Vargas-Ángel (2001)
Galápagos Islands, Ecuador		
Onslow Island (Devil's Crown)[a]	7330 cal year BP	Toth (2013)

All records were obtained from radiocarbon dating of basal samples of cores except for the record from Clipperton Atoll. The Clipperton date was approximated based on estimates by Carricart-Ganivet and Reyes-Bonilla (1999) of sea-level changes and atoll subsidence. To our knowledge, no bottom dates have been obtained from the bases of coral outcrops on Clipperton Atoll to test these assumptions

[a] Coral formation ~100 m east of Onslow island; this is an unconsolidated biostrome rather than a true reef

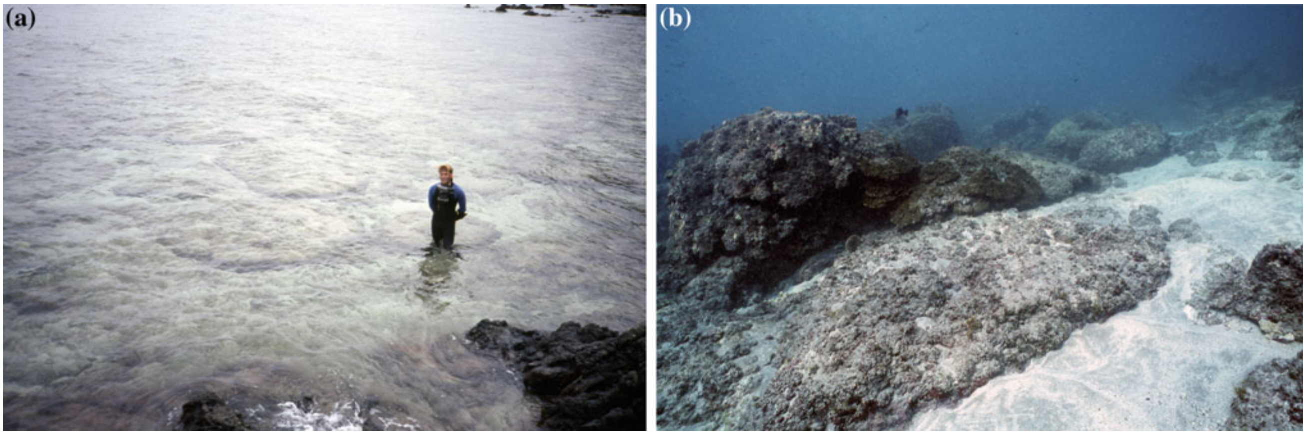

Fig. 6.4 Caño Island reef, Costa Rica, February 1989. **a** *Porites lobata* microatolls on the reef flat. **b** Buttresses of algal-covered metasediment and large *Porites lobata* colonies on the reef slope, 4 m depth (*photo* by I.G. Macintyre)

310 cal year BP). Five framework samples attached to the metasedimentary substrate yielded an older average date of 1838 cal year BP (2-sigma range 2284–1522 cal year BP; Macintyre et al. 1992). These data, along with growth data on the microatolls (Guzmán and Cortés 1989b), show that: (1) the reef, which is now mostly dead, began accreting at least 1500 years ago; and (2) the large *Porites lobata* colonies are not more than 200–300 years old (Macintyre et al. 1992).

6.4.4.4 Cocos Island

Cocos Island (Isla del Coco) is a large, basaltic island associated with several smaller islands, located about 500 km southwest of Costa Rica (5°31′N, 87°3′W; Fig. 6.1). Up to 29 species of scleractinian corals have been reported from Cocos Island (Guzmán and Cortés 1992, 2007), but coral cover is patchy (Bakus 1975). The surfaces of dead coral and basalt generally have a thin coating of crustose coralline algae and filamentous algal turfs. Interlocking, massive colonies, which are primarily *Porites lobata*, form an incipient framework in Chatham Bay near Ulloa Island and extensive coral reefs in an embayment south of Pájara Island, and along other sites on the north side of Cocos Island (see Fig. 5.14 in Chap. 5, Glynn et al.).

The reefs of Cocos Island experienced catastrophic coral mortality during the 1982–83 El Niño warming event, and by 1987 living coral cover was only 3.5 % (Guzmán and Cortés 1992). The dead-coral surfaces were extensively bioeroded by the sea urchin *Diadema mexicanum*. The flanks of large *Porites lobata* mounds have survived (Fig. 6.5), and some of the living surfaces have since regrown over the dead patches (Macintyre et al. 1992).

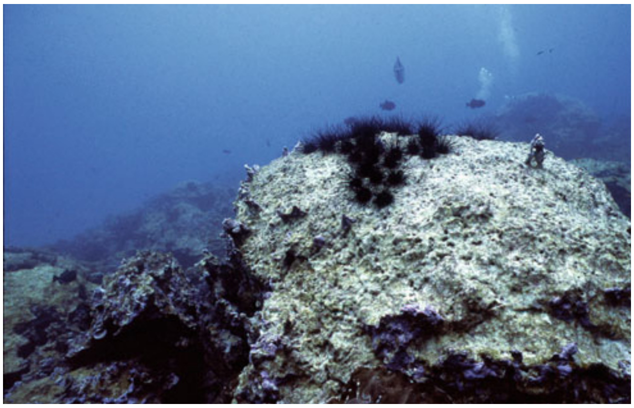

Fig. 6.5 Cocos Island, Costa Rica, 6 m depth, September, 1987. A large colony of *Porites lobata* with its dead surface extensively bioeroded by *Diadema mexicanum* (*photo* by I.G. Macintyre)

Cores were collected from large *Porites lobata* colonies growing around Cocos Island, and bottom samples from these cores were radiocarbon dated. The bases of the longest cores from Chatham Bay (3.1 m penetration) dated to 304 cal year BP (2-sigma range: 473–100 cal year BP) and from Pájara Island (3.0 m penetration) to 455 cal year BP (2-sigma range 626–279 cal year BP; Table 6.1). The dates represent minimum estimates of the timing of reef initiation at these sites because bioerosion has hollowed out the bases of the large colonies (Macintyre et al. 1992). These limited data represent the best records of reef-framework accumulation in the area.

6.4.5 Panama

Some of the best-developed and best-studied reefs in the ETP are found off the Pacific coast of Panama, in the Gulfs of Panama and Chiriquí. Most Panamanian coral reefs are fringing, *Pocillopora*-dominated reefs typical of the ETP region; however, reefs dominated by massive corals are not uncommon. Like many areas of the ETP, the most extensive reefs are found in the sheltered embayments of offshore islands (Glynn and Maté 1997).

Coral reefs in the Gulf of Panama and Gulf of Chiriquí are subjected to distinct oceanographic and ecological conditions. The Gulf of Panama experiences strong, wind-driven, seasonal upwelling, whereas upwelling is weak to absent in the Gulf of Chiriquí (D'Croz and O'Dea 2007; Alexander et al. 2012; Toth et al. 2012; Fig. 6.6). Physical oceanographic conditions appear to play a dominant role in the rate of reef-framework accumulation in the two gulfs, although other limiting factors come into play as well, including the aerial exposure of reef flats during extreme-low tides (Fig. 6.7) and, in the Gulf of Chiriquí, coral mortality from predation by *Acanthaster planci* (Glynn 1976).

6.4.5.1 Gulf of Chiriquí

The reef at Uva Island (7°48′N, 81°45′W) is one of the best-studied reefs in the ETP. This 2.5-ha reef, located in the northern embayment of the island, is dominated by pocilloporid corals, but massive *Gardineroseris planulata* colonies are also abundant (Fong and Glynn 1998; Maté 2003).

Fig. 6.6 Satellite image of sea-surface temperature anomalies during seasonal upwelling, Pacific Panama (modified from Toth et al. 2012)

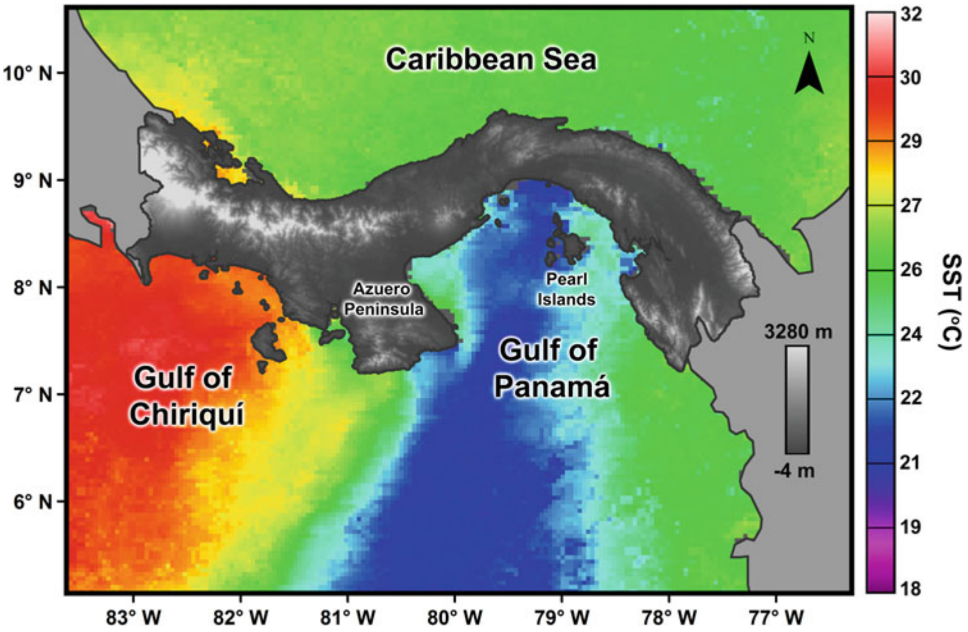

Fig. 6.7 Low tidal exposure of the Uva Island reef flat during the 2010 La Niña, September 2010 (*photo* by L.T. Toth)

Fig. 6.8 *Pocillopora*-dominated reef front at Secas Study Reef, 3 m depth, July 2011. The steep sides of the reef framework are the result of slumping and/or calving of large pocilloporid blocks (*photo* by J.W. Hobbs)

An 11-m drill-core collected from the reef flat suggests that reef initiation in the Gulf of Chiriquí occurred between 6180 and 5810 cal year BP [2-sigma range, calibrated from Glynn and Macintyre (1977); Tables 6.1, 6.2]. Reef-probing at Coiba, Canales de Tierra, and Cavada Islands showed similar degrees of Holocene framework accumulation (up to 9.4, 10.4, and 9.2 m, respectively), but the coastal coral reef at Ensenada de Muertos revealed only 7.9 m of accumulation (Glynn and Macintyre 1977).

The best-developed reef in the Gulf of Chiriquí, Secas Study Reef, occurs along the northwest coast of an unnamed island (7°57′N, 82°0′W) in the Secas Islands group (Glynn and Maté 1997; Maté 2003). This 7.6-ha fringing reef is one of the largest reefs in the ETP (Maté 2003). The Secas Study Reef is dominated by blocks of interlocking colonies of *Pocillopora* spp., many of which have slumped or been overturned by wave action (Glynn and Maté 1997; Fig. 6.8). Glynn and Macintyre (1977) probed 13.4 m into the reef, which suggests that reef accretion has been especially rapid at this site (Table 6.1).

The maximum rates of Holocene reef accretion reported by Glynn and Macintyre (1977) in the Gulf of Chiriquí were all representative of the last thousand years of reef deposition. Centennial-scale records from probing and framework excavation at the Secas Study Reef suggested that accretion rates were as rapid as 2 m/100 year over short time intervals, and averaged 0.74–0.75 m/100 year. At Uva Island reef, centennial-scale rates of reef accretion averaged 0.42 m/100 year. When millennial-scale reef sequences from drill-cores are considered, however, reef accretion is considerably lower. Glynn and Macintyre (1977) calculated an average accretion rate of only 1.6 m/1000 year for the reef at Uva Island over the last six millennia.

We collected a series of push-cores from nearby Canales de Tierra Island (Fig. 6.10). At this site, average accretion rates were ∼1 m/1000 year (Toth et al. 2012; Toth 2013); however, our detailed reconstructions of reef development at Canales de Tierra, as well as at Contadora and Iguana Islands in the Gulf of Panama, suggest that previous measurements may have underestimated reef accretion in this region. The reefs at Canales de Tierra, Iguana, and Contadora Islands experienced a 2500-year shutdown in reef development beginning ∼4100 cal year BP, most likely as a result of enhanced ENSO activity (Fig. 6.9; Toth et al. 2012, 2015). Accretion in Pacific Panama was not always slow; it just appears to have been slow on average because of a prolonged hiatus in reef growth. Indeed, millennial-scale rates of vertical accretion during times of active reef growth at Canales de Tierra were ∼2.4 m/1000 year (Toth 2013). Interestingly, the hiatus in reef development at these sites in Pacific Panama coincided with the period of limited reef accretion in Golfo Dulce, discussed above.

Accretion in the Gulf of Chiriquí during times of active reef growth was only slightly lower than the rate of 3–4 m/1000 year reported for an *Acropora palmata*-dominated reef at Galeta Point, on the Caribbean coast of Panama, but it was comparable to average accretion rates on most Caribbean reefs (Macintyre and Glynn 1976, and references therein; Toth et al. 2012). The highest accretion rate for the Caribbean, measured for uncemented Alacrán Reef, Mexico, was 12 m/1000 year, which, although similar to centennial-scale accretion rates in the Gulf of Chiriquí and Costa Rica (discussed above; Cortés et al. 1994), was much more rapid than any millennial-scale accretion rate measured in the ETP (Macintyre et al. 1977). Accretion in the Gulf of Chiriquí was also generally lower than in most parts of the western Pacific (Montaggioni 2005, and references therein; Toth et al. 2012).

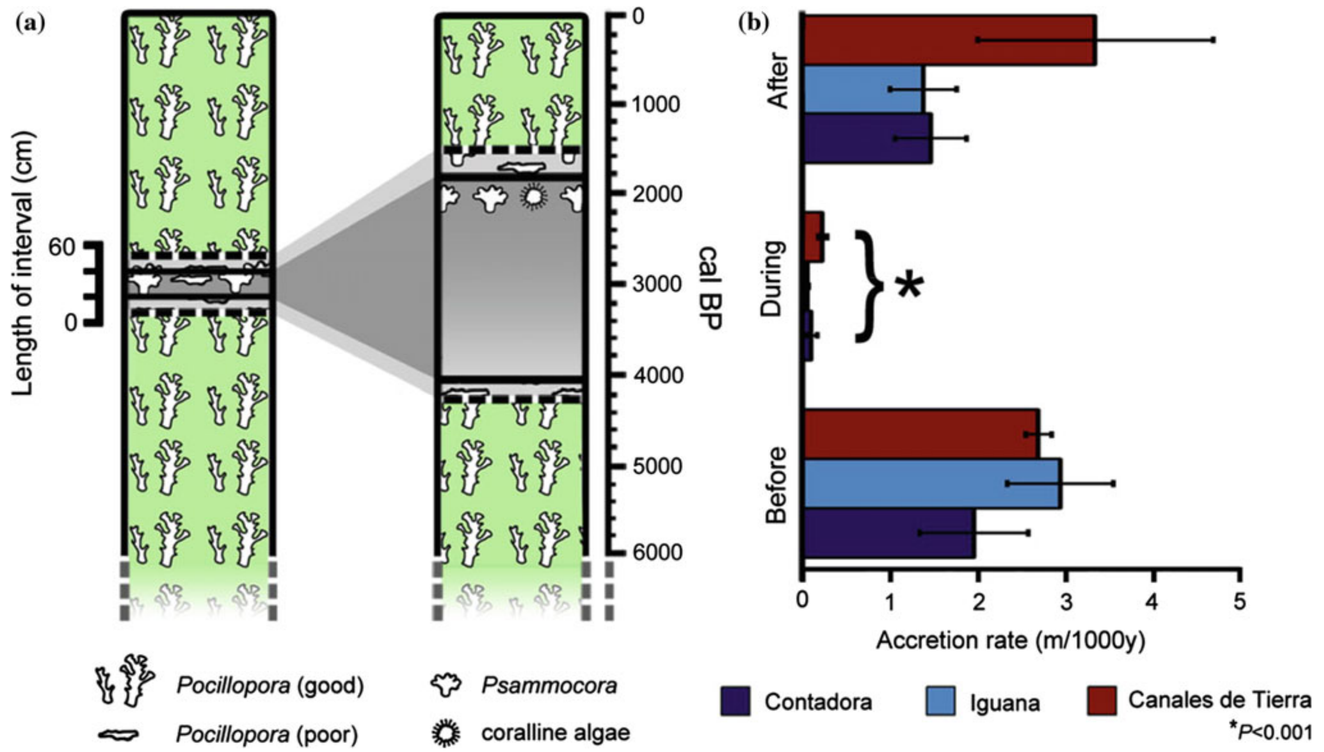

Fig. 6.9 Graphical representation of hiatus in reef development in three locations in Pacific Panama. **a** Composite core log. Green shading with *Pocillopora* in good taphonomic condition indicates periods of active reef growth. Gray shading with *Pocillopora* in poor condition, and presence of *Psammocora* and coralline algae indicate interrupted reef accretion. The length of the hiatus (*gray shading*) is shown in depth in the reef framework (*left*) and expanded to calibrated calendar years before 1950 (*right*). Dark-gray shading represents the most conservative time span for the hiatus; light-gray shading shows the maximum range for all three sites. Note absence of coral dating within all but the beginning and end of hiatus. **b** Mean accretion rates before, during, and after the hiatus. Colors represent upwelling strength: no upwelling (*maroon*), intermediate upwelling (*light blue*), and strong upwelling (*dark blue*). Error bars are standard errors; asterisk indicates significant difference from the other groups (ANOVA, $p < 0.001$). Modified from Toth et al. (2012); reprinted with permission from AAAS

6.4.5.2 Gulf of Panama

Coral reefs in the Gulf of Panama are similar in composition to those in the Gulf of Chiriquí; however, their distribution is strongly influenced by seasonal upwelling (Glynn and Stewart 1973). Most of the coral reefs in the Gulf of Panama are found in the Pearl Islands, located 60 km southeast of Panama City (Fig. 6.1; Glynn and Maté 1997). These islands are exposed to the full force of upwelling currents flowing across the Panama shelf (Toth et al. 2012; Toth 2013), and, therefore, coral reefs in this region are primarily restricted to the sheltered embayments on the northern and eastern sides of the islands (Glynn and Stewart 1973).

Coral assemblages on the exposed sides of the islands are generally incipient structures with little or no geologic history. For example, we collected a push-core from the 1.9-ha pocilloporid reef on the south side of Mogo Mogo Island (8° 33′N, 79°1′W) in the summer of 2009. Despite the high coral cover and large spatial extent of the reef, we were only able to core a maximum of 0.5 m into the coral framework before reaching bedrock. The modern radiocarbon date from a coral sample at the bottom of the core indicated that the reef had been growing for 50 years or less.

In contrast, significant framework accumulations have been observed at some of the more sheltered sites in the Pearl Islands. Based on reef-probing by Glynn and Macintyre (1977), the 5.6-m-thick reef at Saboga Island has the greatest framework accumulation in the Pearl Islands (8°37′N, 79°3′W; Table 6.1). This 14.3-ha, *Pocillopora*-dominated reef is the largest, best-studied reef in the Pearl Islands (Glynn and Maté 1997). Although living coral once covered over 90 % of the reef surface (Glynn 1976), El Niño-related mortality in 1982–83 resulted in a significant reduction in coral cover at the site (Glynn et al. 2001). Today, living coral cover at the Saboga Island reef is patchy, and most living coral is restricted to the outer edge of the reef.

We collected 13 push-cores from the reef at Saboga Island between 2005 and 2009 (Fig. 6.10). Analysis of subfossil corals in the cores suggests that reef development was spatially patchy and temporally sporadic throughout the Holocene history of the reef. In 2009, we collected two cores

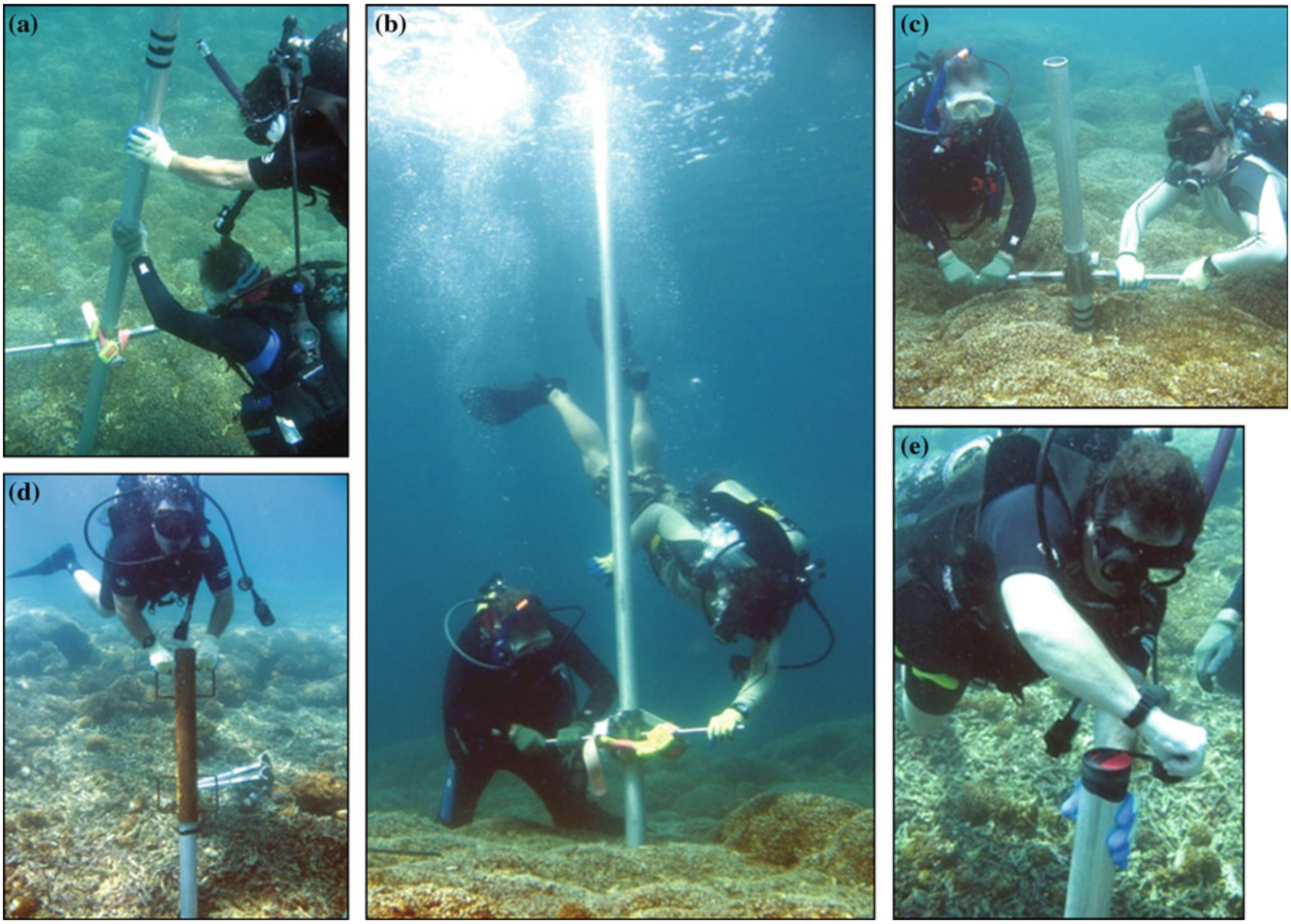

Fig. 6.10 Montage of push-core sampling, Iguana Island reef, September 2007. **a** positioning core tube in reef. **b** core tube in upright position in the reef. **c** adjustable core handles used to rotate core tube into reef framework. **d** hammer-weight for forcing core tube into reef framework. **e** core tube fully penetrated into reef and being prepared for extraction. *Photos* by R.B. Aronson and S.V. Vollmer

that penetrated approximately 3.6 m into the *Pocillopora* framework and reached the basaltic bedrock at the base of the reef. The oldest sections of the cores were dominated by fragments of branching coralline algae, which imply that little or no coral was present during the earliest stages of reef development. Bottom dates from these cores suggest that the pocilloporid reef at this site was established approximately 4348 cal year BP (2-sigma range 4558–4131 cal year BP; Table 6.2). This date is comparable with the bottom date obtained by Glynn and Macintyre (1977) from a drill-core extracted from the reef [2-sigma range 4549–4168 cal year BP, calibrated from Glynn and Macintyre (1977) using the local reservoir correction for the Gulf of Panama]. The timing of reef establishment at Saboga is well after the putative time of shelf-flooding in the region, 7000 years ago (Lighty et al. 1982; Toscano and Macintyre 2003), suggesting that conditions inimical to reef growth persisted for some time after flooding. Based on radiocarbon dating of core samples, Glynn and Macintyre (1977) found the average accretion rate at Saboga Island reef over the last 4500 year to be approximately 1.3 m/1000 year. This millennial-scale accretion rate was less than the 1.6 m/1000 year they reported for Uva Island, which may be due to the negative influence of upwelling on reef development in the Gulf of Panama (Glynn and Macintyre 1977).

Playa Larga reef (8°37′N, 79°1′W), located along the northeast coast of Contadora Island, is less than 3 km from the reef at Saboga Island; however, the Holocene history of reef development at Contadora is very different from that at Saboga. Playa Larga reef is 11.7 ha in area. The reef is dominated by pocilloporid corals, but *Porites lobata* is also common, especially at the southern end of the reef (Glynn and Maté 1997). Probing of the seaward edge of the reef indicated that the maximum framework accumulation is approximately 4.6 m (Table 6.1; Glynn and Macintyre 1977). The deepest push-core we collected at this site, which encountered bedrock, had a very similar penetration depth, namely 4.4 m. Although there is less framework accumulation at the Playa Larga reef than at the Saboga Island reef, a radiocarbon date from the bottom of the deepest push-core we collected at Playa Larga showed that the reef initiated around 6956 cal year BP (2-sigma range 7094–6645 cal year BP), which is more than 2000 years before reef initiation at Saboga Island (Table 6.2). The cores from Playa Larga and Saboga were collected in approximately the same water depth and within the same reef zone, but the reef at Playa Larga apparently began growing shortly after shelf-flooding.

The reef at Contadora experienced the same 2500-year hiatus in development as the reef at Canales de Tierra in the Gulf of Chiriquí (Fig. 6.9). Trends in elemental and isotopic composition of *Pocillopora* branches from a core collected at Contadora suggest that a regime of increased upwelling and precipitation at the onset of the hiatus 3800–3600 cal year BP provided the initial trigger for reef shutdown (negligible to zero accretion). Those conditions indicate an enhanced La Niña regime. Because the hiatus also occurred in the Gulf of Chiriquí, where there is no upwelling, climatic cooling and enhanced turbidity (light limitation) from high precipitation most likely drove regional reef collapse at this time (Toth et al. 2012, 2015). Whereas ENSO variability was the ultimate cause of reef shutdown, upwelling exerted a secondary influence in the Gulf of Panama, leading to a more protracted hiatus at Contadora compared with Canales de Tierra in the Gulf of Chiriquí (Toth et al. 2012).

The overall rate of reef accretion during the Holocene Epoch was lower at Contadora than in the Gulf of Chiriquí: 0.7 versus 1 m/1000 year. Overall accretion rates at Contadora were also lower than at Saboga: 0.7 versus 1.6 m/1000 year; however, when only periods of active reef development are considered, the accretion rate at Contadora was 1.6 m/1000 year, equivalent to the rate at Saboga (Toth 2013).

The other coral reefs probed in the Pearl Islands Archipelago during Glynn and Macintyre's (1977) regional survey, Pedro González and Cañas Islands, had similar levels of Holocene framework accumulation: 4.3 and 4.9 m, respectively. Overall, framework accumulation is significantly lower in the Gulf of Panama than in the Gulf of Chiriquí (independent t-test: $t = 5.664$, df = 9, $P < 0.001$), likely a result of the lower accretion rates in the former area.

The only large coral reef in the Gulf of Panama beyond the Pearl Islands is on the west side of Iguana Island (7°37′N, 80° 0′W), 4 km east of the Azuero Peninsula. The 16-ha reef at Iguana Island is the largest reef in the Gulf of Panama and was declared a Wildlife Reserve in 1981. The shallow habitats of the reef are dominated by pocilloporid corals, but massive corals, including *Porites lobata* colonies up to 400 years old, are abundant at greater depths (Guzmán et al. 1991). Iguana Island experiences some impacts of the annual upwelling in the Gulf of Panama, but upwelling is less intense in this part of the gulf. Based on reef probing, the maximum framework thickness at Iguana Island is 6.1 m (Table 6.1; Glynn and Macintyre 1977). This suggests that the reef at Iguana Island is somewhat better developed than the reefs in the Pearl Islands; however, reef thickness is still greater in the Gulf of Chiriquí (one-sample t-test: $t = 4.324$, df = 5, $P = 0.012$).

We collected 8 push-cores from the reef at Iguana Island in 2006 and 2007. The maximum radiocarbon age from a sample of *Psammocora stellata* at the base of one of our cores indicates that the reef at Iguana Island began accreting around 6762 cal year BP (2-sigma range 6920–6621 cal year BP), at about the same time as the reef at Playa Larga (Table 6.2). The reef at Iguana stopped growing ~4100 cal year BP and vertical accretion was minimal over the next 2500 year, as was the case at Contadora and Canales de Tierra (Fig. 6.9; Toth et al. 2012). Millennial-scale accretion rates at Iguana outside this hiatus were ~1.8 m/1000 year, which are slightly higher than at Contadora but lower than at Canales de Tierra in the Gulf of Chiriquí. The growth rate of *Pocillopora damicornis* is approximately 20 % lower in the Gulf of Panama than in the Gulf of Chiriquí, and this difference is most pronounced during the upwelling season (Glynn 1977). The suppression of pocilloporid growth by upwelling may explain the millennial-scale differences in reef accretion between the two gulfs. In summary, reefs off the Pacific coast of Panama are best developed in the Gulf of Chiriquí, intermediate at Iguana Island, and least developed in the Pearl Islands. These differences reflect the influence of the gradient in upwelling across the three locations.

6.4.6 Colombia

Significant reef formations have been reported in several areas of Pacific Colombia. In the northern part of the country, coral reefs can be found in the Gulf of Cupica (6° 32′N, 77°21′W; Fig. 6.1) and Ensenada de Utría (6°4′N, 77° 23′W; Fig. 6.1). Tebada, the largest reef in the Gulf of Cupica (4.5 ha), is currently dominated by slow-growing *Psammocora* sp.; nevertheless, probing of the reef suggests that Tebada has a Holocene carbonate accumulation of at least 4 m (Table 6.1; Zapata and Vargas-Ángel 2003). The best-developed reef in Ensenada de Utría is the 10.5-ha, *Pocillopora*-dominated reef at La Chola (Vargas-Ángel 1995, 2001; Zapata and Vargas-Ángel 2003). According to the results of probing and coring by Vargas-Ángel (2001), the unconsolidated *Pocillopora* framework at La Chola is 2–4.5 m thick and has been accumulating continuously for the last 2000–3000 years. Average accretion rates at La Chola were 2.5 m/1000 year (Vargas-Ángel 2001), which is similar to rates observed on reefs in other non-upwelling regions in the ETP (i.e., Golfo Dulce and the Gulf of Chiriquí).

Records of large coral aggregations have also been reported around the oceanic island of Malpelo (4°0′N, 81° 36′W; Fig. 6.1), located almost 500 km from the Colombian coast (Birkeland et al. 1975; Garzón-Ferreira and Pinzón

1999; Zapata and Vargas-Ángel 2003). The clear water surrounding Malpelo Island provides good conditions for reef development (Garzón-Ferreira and Pinzón 1999), and corals can be found along the island's slope to a depth of 30 m (Birkeland et al. 1975). Despite the high coral cover at Malpelo (15–89 %; Birkeland et al. 1975; Garzón-Ferreira and Pinzón 1999), there is no evidence of accumulation of fossil and subfossil corals, possibly due to the steep slope of the subtidal substrate (Birkeland et al. 1975). It is generally agreed that the coral aggregations at Malpelo cannot be considered true coral reefs (e.g., Birkeland et al. 1975; Zapata and Vargas-Ángel 2003).

The majority of known coral reefs in Pacific Colombia are found around Gorgona Island (2°59′N, 78°12′W; Fig. 6.1), approximately 35 km off the South American coast (Glynn et al. 1982; Prahl 1986; Zapata and Vargas-Ángel 2003). As at Malpelo Island, the water surrounding Gorgona Island is clear, and corals can occur to depths of 30 m (Zapata and Vargas-Ángel 2003). Fringing coral reefs are best developed on the east side of the island; however, cementation of framework by coralline algae only occurs on the island's western face (Glynn et al. 1982). Most of the reefs at Gorgona display patterns of coral zonation typical of the ETP, with pocilloporids dominating shallow substrates and massive *Porites*, *Pavona*, and *Gardineroseris* species increasing in abundance with depth (Glynn et al. 1982).

The *Pocillopora* framework of La Azufrada reef, the largest coral reef adjacent to Gorgona Island (11.2 ha; Zapata and Vargas-Ángel 2003), was probed by Glynn et al. (1982) and found to be 8 m thick (Table 6.1). Prahl (1986) suggested that the reef at La Azufrada likely formed after stabilization of sea level in the region, around 2500–3000 years ago. Visual inspection of nearby Pier Reef suggested that Holocene framework accumulation at this reef was 6 m above the seafloor. Framework accumulation at La Gómez and La Ventana formations, also nearby, was only 1 m, suggesting that these structures are incipient reefs (Glynn et al. 1982). The maximum framework thickness of the reefs between Gorgona and nearby Gorgonilla Islet was approximately 2 m, based on visual inspection (Prahl 1986; Zapata and Vargas-Ángel 2003).

6.4.7 Ecuador

6.4.7.1 Mainland Ecuador

Ecuador represents the southern limit of reef development along the ETP mainland, and there are few structural coral reefs in this region. During the 1970s, however, several reefs were described along coastal Ecuador (Glynn 2003). Surface inspections of the 1-ha, *Pocillopora*-dominated fringing reef along the leeward shore of Sucre Island (1°28′N, 80°46′W; Fig. 6.1), off the coast of Machalilla, suggested a Holocene framework accumulation of 3–4 m. Several kilometers south of Machalilla, a similar degree of framework accumulation was estimated for the pocilliporid reef adjacent to Cabuya Beach. When both reefs were revisited in the early 1990s, however, there was very little living coral and much of the existing framework had eroded. This was likely the result of the regional devastation of coral reefs by the 1982–83 El Niño event. The only living reefs currently found near the Ecuadorian mainland occur on the northeast coast of La Plata Island (1°16′N, 81°5′W; Fig. 6.1; see also Chap. 5, Fig. 5.25, Glynn et al.), located 31 km west. These reefs are built primarily by massive coral species, including *Pavona clavus*, *Pavona gigantea*, and *Gardineroseris planulata*, and have vertical accumulations of 2–6 m (Table 6.1; Glynn 2003).

6.4.7.2 Galápagos Islands

The Galápagos Islands are located 1050 km west of the Ecuadorian coast (Fig. 6.1). Due to their equatorial position, the Galápagos are subject to the most extreme consequences of ENSO. El Niño in particular has been a major cause of coral mortality in the Galápagos, most notably during the 1982–83 El Niño event (Glynn and Wellington 1983; Glynn et al. 2001; Glynn 2003; Wellington and Glynn 2007). Prior to the 1982–83 El Niño, small coral reefs could be found at many of the central and southern Galápagos Islands. Due to the high water clarity in most areas, corals occurred to depths of 30 m. Reef development on the western sides of Isabela and Fernandina Islands was limited because of localized upwelling, but small patch reefs and assemblages of non-reef-building corals were found in more sheltered areas of these islands. El Niño-related mortality in the early 1980s resulted in the loss of over 90 % of Galápagos reefs, and there has been very little recovery since [Glynn 2003; but see Glynn et al. (2009, 2015) for examples of rapid coral recovery at the northernmost Darwin and Wenman Islands].

Several studies have been conducted on the coral reefs off the north coast of Floreana Island in the southern Galápagos (1°17′S, 90°26′W; Fig. 6.1). The reef community of Champion Island off the northern coast of Floreana, for example, was reported to be flourishing in 1975 and 1976 (Fig. 6.11a). This reef was dominated by *Pavona* spp. and revealed Holocene framework accumulation of up to 5 m (Table 6.1; Glynn 2003). In 1990, the reefs were almost completely bioeroded by the sea urchin *Eucidaris galapagensis* (Fig. 6.11b) following catastrophic coral mortality caused by the 1982–83 El Niño event. The seascape was reduced to extensively bioeroded *Pavona* skeletons on a knobby coral pavement, covered by filamentous algal turf (Fig. 6.11b; Macintyre et al. 1992).

Prior to 1982, there were reports of a *Pocillopora* reef in the embayment of Onslow Island, north of Floreana—an area known as Devil's Crown (1°13′S, 90°25′ W; Fig. 6.1)—although reef-probing suggested the thickness of

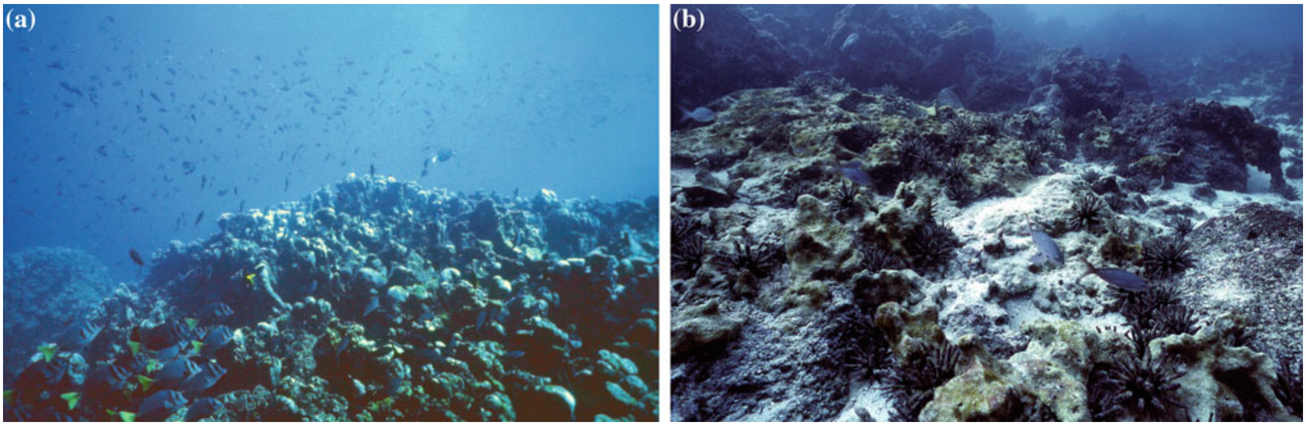

Fig. 6.11 Patch reef off Champion Island, Galápagos Islands before and after the 1982–83 El Niño warming event, 6 m depth. **a** Framework dominated by living *Pavona clavus*, January 1975. **b** Same general area with extensive bioerosion of the reef surface by *Eucidaris galapagensis*, November 1990. *Photos* by P.W. Glynn **a**, and I.G. Macintyre **b**

this reef was less than 1 m (Glynn and Wellington 1983; Glynn 2003). The existing framework was completely bioeroded in the wake of the 1982–83 El Niño disturbance (Glynn 2003). Consequently, in 1990 Macintyre et al. (1992) found no significant reef framework at Devil's Crown. The base of one large, toppled, dead colony of *Pavona gigantea* revealed a radiocarbon date of 488 cal year BP (2 sigma range 600–287 cal year BP), suggesting that a thin reef had been growing at this site for a few hundred years. The reefs at Onslow Island and the north coast of Floreana Island, which were flourishing in 1975 and 1976 (Glynn and Wellington 1983), consisted of scattered, small, living colonies of *Porites lobata* and remnants of reef framework that were bioeroded and covered by crustose coralline algae.

Although the inshore reef of Devil's Crown was destroyed, corals persisted in deeper water offshore after the ENSO events of 1982–83 and 1997–98. Surveys in 1999 revealed that an extensive, unconsolidated coral biostrome, dominated by free-living *Psammocora stellata* and *Diaseris distorta*, had covered the sandy bottom at 13–18 m depth, with living coral cover approaching 80 % in some areas. These deep-water assemblages are apparently more resistant to coral bleaching associated with El Niño conditions than the shallow-water assemblages, considering they survived both the 1982–83 and 1997–98 severe events (Feingold 1995, 2001). Three cores collected from Devil's Crown in 1990–91 (Feingold 1995) were analyzed by Hendrickson (2014). The cores demonstrated pronounced shifts in the relative abundance of *Diaseris distorta* and *Psammocora stellata* through time, which may have been related to past climate change. Core penetrations were approximately 1.45, 1.55, and 1.55 m, and the basal dates of the cores were 7330, 5183, and 5116 cal year BP, respectively (Tables 6.1, 6.2), suggesting that the coral biostromes likely began forming soon after shelf-flooding and accreted at an average rate of 0.002–0.003 m/1000 year to the present.

A few coral reefs have been found adjacent to Isabela Island (Fig. 6.1), the largest island in the Galápagos Archipelago. The most significant record of *Pocillopora* framework accumulation, 3–4 m, was observed in the 1970s off Villamil (1°3′S, 91°4′W; Table 6.1; Fig. 6.1), on the southern coast of Isabela. A 1-m accumulation of *Pavona clavus* was observed on the east coast of Isabela (Glynn and Wellington 1983). Like most coral reefs in the Galápagos, however, these reefs succumbed during and following the 1982–83 El Niño event (Glynn 2003).

The living reef in Urvina Bay (0°24′S, 91°15′W; Fig. 6.1), off the west coast of Isabela Island, is covered with knobby mounds of *Pavona clavus* and *Porites lobata* up to 2 m in vertical relief, which protrude from an algae-covered substrate (Fig. 6.12; Macintyre et al. 1992). *Pocillopora*-

Fig. 6.12 Living colonies of *Pavona clavus* protruding above dense algal cover, Urvina Bay, Galápagos Islands, 2 m depth, November 1990. *Photo* by I.G. Macintyre

framework accumulation at Urvina Bay was estimated at 0.5 m (Glynn and Wellington 1983), although this may have been an underestimate of historical accumulations as the reef was extensively bioeroded (Macintyre et al. 1992). A large, subfossil reef, located in the eastern section of Urvina Bay, was uplifted by 6 m in 1954 as a result of volcanism and magmatic intrusion (Glynn and Wellington 1983; Colgan and Malmquist 1987; Colgan 1990; Dunbar et al. 1994). Observations of the uplifted reef showed that calcareous red algae were the first to colonize Urvina Bay, followed by the free-living coral *Psammocora stellata*. In the final stages of reef development, *Pocillopora* spp. and massive coral species also began to recruit and contribute to the framework (Colgan and Malmquist 1987; Colgan 1990).

The only material available for radiocarbon dating in the uplifted section at Urvina Bay came from coral rubble found at the base of a 12-m diameter, uplifted colony of *Pavona clavus*. This sample indicated that reef growth initiated at least 1000 years ago (Colgan 1991). The massive corals in Urvina Bay revealed numerous skeletal discontinuities, suggesting that these coral assemblages were subjected to severe disturbance events in the past, most likely due to ENSO activity (Glynn and Wellington 1983; Dunbar et al. 1994).

Small accumulations of *Pocillopora* framework, 1 m or less in thickness, were also observed at San Cristóbal (0°48′S, 89°24′W), Española (1°22′S, 89°40′W), Santa Fe (0°49′S, 90°3′W), Fernandina (0°25′S, 91°27′W), Darwin (1°40′N, 92°0′W) and Genovesa (0°19′N, 89°56′W) Islands prior to the 1982–83 El Niño event (Glynn and Wellington 1983). These reefs experienced high levels of bleaching-related mortality in 1982–83, and no pocilloporid reefs have re-established since that time (Glynn 2003). However, at a shallow lagoon near Villamil, Isabela Island, an incipient pocilloporid framework observed recently is forming by asexual propagation (Baums et al. 2014; Feingold and Glynn 2014).

In general, reefs dominated by massive corals were found to have considerably more carbonate accumulation than *Pocillopora*-dominated reefs in the Galápagos Islands. *Porites lobata* reefs off Santiago and Bartolomé Islands had framework accumulations of 2–3 and 4–5 m, respectively (Table 6.1). Bartolomé also had a *Pavona*-dominated reef that was up to 6 m thick, and a 2–3 m thick *Pavona* reef was found at Genovesa (Glynn and Wellington 1983). The vertical accumulation of massive coral skeletons in the Galápagos is comparable to that off the mainland (Glynn and Wellington 1983). Most of the corals on these reefs are now dead and have suffered high levels of bioerosion (Glynn 2003); however, the Darwin Island reef, which was once colonized by both pocilloporid species and massive *Porites lobata*, has shown surprising recovery since the 1982–83 El Niño. Although coral mortality was high, the surviving *Porites lobata* colonies have recolonized the reef since the 1982–83 event; nevertheless, there has been no recovery of *Pocillopora* (Glynn et al. 2009, 2015). This suggests that reefs dominated by massive corals may be more resilient to the impacts of ENSO events, possibly because massive-coral frameworks may be inherently more resistant to the effects of bioerosion. Furthermore, the growth of massive corals is less affected than the branching pocilloporids by upwelling conditions (Manzello 2010), which may be another reason for the high abundance of reefs dominated by massive corals in some parts of the Galápagos Islands.

The rate and extent of reef development in the Galápagos are limited by bioerosion, which is caused primarily by the grazing sea urchin *Eucidaris galapagensis* (Glynn et al. 1979). Although modern growth rates of *Pocillopora* are fairly high in the Galápagos (Glynn and Wellington 1983), the majority of gross carbonate production by pocilloporids is degraded by bioerosion (Glynn et al. 1979). In most areas of the Galápagos, therefore, framework accumulations are relatively thin layers growing atop the basalt bedrock (Glynn and Wellington 1983), and long-term rates of vertical accretion are low.

In summary, nearly all coral reefs in the Galápagos experienced significant loss of framework due to high levels of grazing by *Eucidaris galapagensis* in the wake of the 1982–83 El Niño event (Glynn 2003). It is likely, therefore, that a large portion of the geologic record of coral-reef framework has been degraded and lost. The effects of bioerosion by *Eucidaris galapagensis* are most severe for fragile *Pocillopora* spp. (Glynn et al. 1979), which may explain why most of the pocilloporid reefs in the Galápagos have been reduced to rubble whereas structures built of massive corals are more often partially intact.

6.4.8 Clipperton Atoll

Clipperton Atoll (10°18′N, 109°13′W; Fig. 6.1), located approximately 1100 km west of the Mexican coast, lies at the westernmost edge of the ETP. Because of its isolation, coral diversity is low at Clipperton (Glynn et al. 1996; Glynn and Ault 2000; see Chap. 5, Glynn et al.). Nevertheless, the continuous coral reef that encircles the island, measuring 370 ha in area, is the largest structural reef in the ETP (Dana 1975; Glynn et al. 1996). Water clarity is high compared with other areas supporting reef growth in the ETP (Dana 1975; Glynn et al. 1996), and, as a result, reef development extends to at least 60 m depth (Glynn et al. 1996). In contrast, high turbidity and low light penetration restrict most coral-reef development to depths of 10–15 m or less along the ETP mainland (Dana 1975; Glynn 1976).

Reef-habitats at Clipperton Atoll are dominated by large *Porites* colonies, but monogeneric patches of *Pocillopora* spp. are also present (Glynn et al. 1996). Glynn et al. (1996)

measured living and dead colonies of *Pocillopora* at Clipperton reef and found them to be at least 1–2 m in height, although they suggested that the thickness of Holocene reef accumulation is likely greater than that. Linsley et al. (2000) obtained drill-cores measuring 120, 126, and 245 cm in length from three massive *Porites* colonies on the reef. The basal dates of the cores, 1937, 1947, and 1893 C.E., demonstrated that the growth of *Porites* was rapid at their sampling site. Carricart-Ganivet and Reyes-Bonilla (1999) observed a number of coral terraces approximately 6 m above sea level on Clipperton. Based on the putative sea-level curve for the region, and accounting for subsidence of the atoll, they estimated that these terraces initiated growth approximately 5000 years ago. Their date provides a reasonable minimum estimate for the time of reef initiation at Clipperton Atoll. Another reef terrace, found at approximately 60 m depth, may be the remnant of a shallow fringing reef that formed during a sea-level low-stand in the late Pleistocene (Glynn et al. 1996).

6.4.9 Easter Island (Rapa Nui)

Easter Island, or Rapa Nui as it was first named by colonizing Polynesians, is located in the south-central Pacific, approximately 3750 km west of mainland Chile, to which it belongs (27°07′S, 109°22′W; Fig. 6.1). The coral fauna of Rapa Nui is both geographically and oceanographically isolated from most reefs of the wider Pacific (Glynn et al. 2003; Hubbard and Garcia 2003; Glynn et al. 2007), but the island is generally considered to be the easternmost outpost of the Indo-Pacific bioregion (Glynn et al. 2007; see also Veron et al. 2015). The island is ~2250 km from the Pitcairn Islands group in the central Pacific (24°23′S, 128°19′W), which is more than 1500 km closer than its nearest neighbor in the eastern Pacific: the Galápagos Islands (Glynn et al. 2003, 2007); however, the coral fauna of Rapa Nui is more closely aligned with that of the eastern Pacific than any other bioregion, suggesting that Easter Island should, in fact, be included in the eastern Pacific faunal province (Glynn et al. 2007).

Although coral growth in much of the southeastern Pacific is precluded by low temperatures, the waters surrounding Rapa Nui are warmed by the South Pacific Subtropical Gyre. This warm, subtropical water has allowed extensive coral assemblages to develop around the island (Glynn et al. 2003, 2007; Hubbard and Garcia 2003). Furthermore, because of the high water clarity, corals occur to depths of 60 m (Glynn et al. 2003, 2007; Hubbard and Garcia 2003). There are 13 species of corals living at Rapa Nui (Glynn et al. 2007), but most communities are dominated by *Pocillopora verrucosa* down to 10 m depth and *Porites lobata* in deeper reef zones (DiSalvo et al. 1988; Glynn et al. 2003, 2007; Hubbard and Garcia 2003). The extent of reef development around Rapa Nui is highly variable. Coral cover is low along the southeastern shore due to strong wave action for most of the year, which interferes with coral settlement and growth. In contrast, surveys along the western and northern coasts have revealed that coral cover in some areas can exceed 100 % (Glynn et al. 2003, 2007; Hubbard and Garcia 2003).

True reef development at Rapa Nui is restricted to two leeward-island locations: the Poike Peninsula at the northeastern corner of the island, and Cook Point along the west coast (Glynn et al. 2003; Hubbard and Garcia 2003). At both locations, Hubbard and Garcia (2003) observed *Porites* frameworks representing multiple generations of coral growth. The largest living *Porites* colonies observed were 10 m high, and *Porites* reef frameworks up to 7 m thick were common at these sites (Table 6.1; Glynn et al. 2003; Hubbard and Garcia 2003). During field work at Rapa Nui in 2000, Glynn et al. (2003) collected drill-cores from three relatively small (1–2 m diameter) *Porites lobata* colonies. By measuring the growth rates of these living corals, they estimated that the largest *Porites* colonies were 860–1120 years old. Fossil corals have also been found in some deep-water caves (>50 m depth) along the offshore slopes of the island (DiSalvo et al. 1988), but these corals have not been dated.

6.5 Environmental Controls of Reef Development

6.5.1 Geographic Patterns of Coral-Reef Development in the ETP

The most significant accumulations of *Pocillopora* frameworks are found from about 7–15°N latitude, along the central coastal areas of the ETP (Fig. 6.1; Table 6.1), with the thickest Holocene framework accumulation recorded in the Gulf of Chiriquí, Panama (7°N; Table 6.1). The offshore islands of Clipperton Atoll, Rapa Nui, and to a lesser extent Gorgona Island, also have significant framework accumulation, and because of the high water clarity at these sites corals occur at greater depths than in most regions of the ETP (Table 6.1; Glynn et al. 1982; Carricart-Ganivet and Reyes-Bonilla 1999).

At the extreme northern and southern limits of the region—Mexico and Ecuador—most corals occur as constituents of incipient reef assemblages, and few well-developed reefs can be found (Glynn 2003; Reyes-Bonilla 2003). Framework accumulation is also minimal in the Galápagos Islands, where environmental disturbances are most extreme. Few records from Galápagos reefs have reported *Pocillopora* frameworks thicker than 1 m, and the only significant frameworks consist of isolated patches of massive corals (Glynn and Wellington 1983; Glynn et al. 2009).

6.5.2 Wave Exposure

Throughout the ETP, coral reefs are primarily restricted to sheltered embayments (e.g., Glynn and Stewart 1973; Dana 1975; Glynn and Macintyre 1977; Glynn et al. 1983; Cortés 1990b; Guzmán and Cortés 1992; Glynn and Leyte-Morales 1997; Glynn and Maté 1997). This distributional pattern is due in large part to the protection from wave exposure these areas provide (Dana 1975; Glynn and Maté 1997). At Rapa Nui, for example, few corals are found along the south-eastern shore, where wave energy is highest (Glynn et al. 2003; Hubbard and Garcia 2003). Calm, sheltered environments are conducive to the initiation of reef growth and its continuation for several reasons. First, the majority of reefs in the ETP are dominated by pocilloporid corals, and because there is little cementation of reefs in the region (Macintyre and Glynn 1976; Glynn and Macintyre 1977; Manzello et al. 2008), strong wave action can dislodge existing frameworks, precluding significant carbonate accumulation. Calm water also facilitates sedimentation, allowing a buildup of entrained sediments that can stabilize reefs. Reef accretion by carbonate production and sedimentation may in turn extend the habitable shelf area, allowing for further reef development.

6.5.3 Tides and Turbidity

Tidal amplitudes in the ETP range from ~0.5 m off the coast of Mexico and offshore oceanic islands (Sachet 1962; Glynn and Maté 1997; see Chap. 3, Fiedler and Lavín) to as much as 7 m in Pacific Panama (Glynn 1976). The large tidal ranges in many parts of the ETP are thought to be an important control on reef development in the region (Glynn 1976; Glynn and Macintyre 1977; Glynn and Maté 1997). Two important impacts of tidal fluctuations on reef development are subaerial exposure of corals during extreme low tides and high turbidity associated with tidal flushing.

Subaerial exposure is most common during the spring tides of La Niña years, when mean sea level in the ETP is reduced (Fig. 6.7; Eakin and Glynn 1996). Subaerial exposure can have a major impact on reefs (Glynn 1976; Eakin and Glynn 1996); Glynn (1976) reported coral mortality of up to 70 % on some reefs after a spring tidal cycle of reef exposures.

Although it is clear that subaerial exposure can cause significant damage in the short term, the high turbidity associated with large tidal amplitudes (Glynn 1976), as well as upwelling (discussed below; Glynn and Stewart 1973) and high seasonal precipitation (Dana 1975), may have an even greater impact on long-term reef development in the region. For example, the depauperate coral assemblages and, in some cases, the complete inhibition of coral development in some areas of the Great Barrier Reef, have been attributed to the elevated turbidity associated with large tidal ranges (Kleypas 1996; van Woesik and Done 1997). High turbidity controls reef development by limiting the amount of light that reaches the phototrophic reef-building corals (Kleypas 1996, 1997; Kleypas et al. 1999a). Light limitation restricts reef development to depths of 10–15 m in many parts of the ETP (Dana 1975; Glynn 1976), whereas regions with low turbidity, such as Clipperton Atoll, Rapa Nui, and Malpelo Island, can support coral growth to 30 m depth and deeper (Glynn et al. 1996; Zapata and Vargas-Ángel 2003).

6.5.4 Upwelling

Seasonal upwelling in the Gulfs of Tehuantepec, Papagayo, and Panama, and equatorial upwelling in some parts of the Galápagos Islands, are associated with the intrusion of cold, nutrient-rich waters into shallow, coastal areas (e.g., Dana 1975; Glynn et al. 1983; D'Croz and O'Dea 2007; Alexander et al. 2012; see Chap. 3, Fiedler and Lavín). Growth rates of pocilloporid corals are reduced during the upwelling season in these areas (Glynn and Stewart 1973); therefore, overall growth rates of *Pocillopora* spp. are generally higher on reefs not exposed to upwelling (Glynn 1977). Interestingly, upwelling does not appear to be as detrimental to the growth of massive corals (Jiménez and Cortés 2003; Manzello 2010).

The negative impact of upwelling on pocilloporid corals is primarily due to the reduction of growth and calcification as a result of low sea temperatures (Glynn and Stewart 1973; Glynn 1977), but enhanced nutrient inputs during upwelling can also be problematic. Elevated levels of some nutrients can be detrimental to coral growth and calcification (Kinsey and Davies 1979; Hallock and Schlager 1986), although inorganic nutrients have also been shown to be beneficial to coral growth (Adkinson et al. 1995; Jiménez and Cortés 2003). Increases in nutrients lead to increases in regional primary productivity (Glynn and Stewart 1973; Martínez et al. 2006; D'Croz and O'Dea 2007), and the resultant plankton blooms increase water turbidity (Glynn and Stewart 1973). High nutrients can also increase the competitive ability of macroalgae and suspension feeders on reefs (Glynn and Stewart 1973; Birkeland 1977; Highsmith 1980). Furthermore, upwelled waters have low pH relative to surface waters, which has resulted in a reduction of the carbonate saturation state in the ETP generally (Manzello et al. 2008). This condition may render reefs of the ETP vulnerable to the impacts of ocean acidification, expected to increase with future global climate change (Kleypas et al. 1999b; Guinotte et al. 2003; Manzello et al. 2008). Given the negative impacts of upwelling on modern coral reefs in the ETP, it is not altogether surprising that upwelling was also important in structuring coral reefs of the past.

Records from coral reefs throughout the ETP indicate that upwelling exerted an important influence on development during the Holocene. Generally, where modern corals persist despite the influence of seasonal upwelling—in the Gulf of Panama, for example—reef development is limited to embayments where the corals are sheltered from the full force of oceanic influences (Glynn and Stewart 1973). Similarly, coral-reef development at Isabela and Fernandina Islands in the Galápagos is primarily restricted to the eastern sides of the islands, where upwelling is less influential (Glynn 2003). In both Panama and Costa Rica, reefs are better-developed, with thicker accumulations of *Pocillopora* frameworks, in non-upwelling areas compared with areas that experience upwelling (Table 6.1; Glynn and Macintyre 1977; Glynn et al. 1983; Macintyre et al. 1992; Cortés et al. 1994). An interesting exception is the Huatulco reef tract in the Gulf of Tehuantepec, one of Mexico's major upwelling centers, which supports greater framework accumulation than the non-upwelling regions (Table 6.1; Glynn and Leyte-Morales 1997).

Although upwelling has limited the magnitude of framework accumulation in the ETP, it may not have significantly reduced long-term accretion rates in the region. We found that upwelling did not influence long-term rates of reef accretion within certain favorable intervals—before and after the observed hiatus in reef development—at Contadora, Iguana, and Canales de Tierra Islands in Pacific Panama. Millennial-scale rates of reef accretion within these periods were not significantly different among sites (Toth et al. 2012; Toth 2013).

Upwelling regimes also did not impact the timing of reef initiation. Despite having significantly thicker frameworks than reefs in the Gulf of Panama, reefs in the non-upwelling Gulf of Chiriquí initiated at least 1000 years later. It is possible therefore, that upwelling was less important in controlling reef development in the early Holocene than at present. Conversely, more intense upwelling during certain periods may have precluded reef development in some areas. In northwestern Costa Rica, which experiences the most protracted and intense seasonal upwelling in the ETP, all reefs have experienced nearly complete mortality in recent centuries, possibly due to enhanced upwelling activity (Glynn et al. 1983). Upwelling also resulted in a longer hiatus in reef development in the Gulf of Panama relative to the Gulf of Chiriquí (Toth et al. 2012, 2015).

Overall, the effects of upwelling on coral-reef development in the ETP are mixed. Upwelling is an important control on the distribution of reefs in the region. Moreover, in many areas, reefs exposed to upwelling have significantly thinner accumulations of Holocene reef-framework. Nevertheless, over millennial scales, upwelling may have been less important in determining long-term rates of reef accretion than previously thought.

6.5.5 ENSO

In recent years, ENSO has devastated coral reefs throughout the ETP. El Niño-related coral mortality, especially during the 1982–83 and 1997–98 events, drastically reduced coral cover (Glynn et al. 2001; Jiménez et al. 2001). In many regions, but most prominently in the Galápagos Islands, the increase in bioerosion after these events has led to significant losses of reef frameworks (Glynn 1988; Eakin 1992; Reaka-Kudla et al. 1996; Fonseca 1999; Glynn et al. 2015). La Niña can be equally problematic for reefs of the ETP. Lowered sea level during La Niña events leads to more frequent subaerial exposure of reefs (Glynn 1976; Eakin and Glynn 1996). In some parts of the ETP, La Niña can also enhance seasonal upwelling events, causing cold shock, coral bleaching and mortality (Poveda et al. 2006; Banks et al. 2009; Alexander et al. 2012).

The dynamics of ENSO have not been constant during the Holocene, and it is likely that its impacts have at times been more severe than at present (e.g., Moy et al. 2002; Riedinger et al. 2002; Toth et al. 2012, 2015). We showed that past increases in ENSO variability ultimately led to a 2500-year collapse of coral-reef ecosystems in Pacific Panama (Toth et al. 2012, 2015; Toth 2013). Our reconstructions demonstrate that ENSO variability was likely the most important control of Holocene reef development in the ETP.

6.6 Summary

Coral reefs of the ETP have long been considered depauperate and poorly-developed compared with other regions of the world (Cortés 1993, 1997; Veron 1995). Despite the relatively low coral diversity and geographic isolation of the ETP (Veron 1995; Glynn and Ault 2000), well-developed coral reefs have been discovered throughout the region in recent decades (e.g., Glynn and Macintyre 1977; Glynn et al. 1982, 1983; Glynn and Wellington 1983; Glynn and Leyte-Morales 1997; Carricart-Ganivet and Reyes-Bonilla 1999; Cortés and Jiménez 2003; Reyes-Bonilla 2003; Zapata and Vargas-Ángel 2003). Although coral reefs in the ETP are generally small in size (Dana 1975; Glynn and Macintyre 1977; Cortés 1997; Glynn and Maté 1997) and restricted to sheltered habitats (Dana 1975; Glynn and Stewart 1973; Glynn et al. 1983), reef accretion in the region has been rapid and has persisted for millennia. Indeed, the maximum levels of Holocene framework accumulation in the ETP—on the order of 10–15 m—rival the thickness of reefs in the western Atlantic [Macintyre and Glynn (1976) for Panama; Macintyre et al. (1977) for Mexico; Westphall (1986) for Belize; Hubbard et al. (2005) for St. Croix; Greer et al. (2009) for the Dominican Republic]. In Panama, both short- and long-term rates of reef accretion were comparable across the Pacific and Caribbean sides of the Isthmus (Glynn and Macintyre 1977; Macintyre and Glynn 1976). Although many reefs in the ETP appear to have initiated only in recent millennia (Cortés 1997), reef development at some locations began as early as 6000 to nearly 7000 years ago, corresponding to the time of reef initiation in the Caribbean, but later than elsewhere in the central and western Pacific (Macintyre 2007; Montaggioni and Braithwaite 2009).

In many ways the trends of Holocene reef development in the ETP are more similar to other regions of the world than originally envisaged; however, differences in the histories of reefs within and across oceanic regions are rapidly becoming moot. The globalization of environmental perturbations in recent decades, most critically rising temperatures, is killing framework-building corals—or at the very least slowing their growth and depositional rates—and homogenizing the composition of living reef assemblages (Hoegh-Guldberg et al. 2007; Pandolfi et al. 2011). The loss of framework-building corals threatens to decelerate vertical accretion at a time when sea-level rise is accelerating, potentially compromising the viability of coral reefs and the ecosystem services they provide (Alvarez-Filip et al. 2013; Perry et al. 2013). Although well-developed coral reefs have persisted in a few locations in the ETP for millennia, the future of coral-reef growth in the region remains uncertain.

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