

Chapter 1

Coral Research in the Galápagos Islands, Ecuador

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Abstract This chapter summarizes the scientific knowledge of scleractinian corals in the Galápagos Archipelago. A general introduction to coral biology is followed by a brief history of coral research in the islands. Subsequent sections discuss responses of corals to broad-scale impacts, anthropogenic stress on Galápagos corals, and recommendations for management of this important resource. Following an initial period (1835–1960s) of cataloging the species present in the Galápagos Islands, research on coral ecology was initiated by Wellington in the 1970s. Glynn and Wellington more thoroughly examined the surprising abundance and distribution of corals and reef frameworks in the 1980s. Glynn and other workers then documented mass mortalities of corals due to the 1982–1983 ENSO disturbance. Subsequent research focused upon this natural phenomenon and its effect on coral distribution, ecology, and physiology. Most recently, resilience and recovery of coral populations were reported. Compared to most other regions, there is little anthropogenic impact to corals in the Galápagos Islands. However, climate change and ocean acidification have effects, and there is evidence of impacts associated with fisheries and tourism. Recommendations for management decisions conclude this chapter.

Introduction

This chapter summarizes the scientific knowledge of scleractinian corals in the Galápagos Archipelago, providing a review of prior research and a synthesis of new and emerging issues that are relevant to the Galápagos Marine Reserve. There are four sections in this chapter: (1) introduction, including a distinction between coral communities and coral reefs; (2) a brief history of coral research in the islands;

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(3) responses of corals to broad-scale impacts with particular focus on El Niño-Southern Oscillation (ENSO) activity; and (4) anthropogenic stress on Galápagos corals and recommendations for management.

The Galápagos Archipelago sits astride the equator at approximately 090° W longitude at the confluence of several major oceanic currents. Cool water flows from east to west via the South Equatorial Current (as a westward extension of the Peru Coastal Current and Peru Oceanic Current) and from west to east via the subsurface Equatorial Undercurrent (Cromwell Current). The first set of currents creates centers of upwelling along the continental coast, and the Cromwell Current drives upwelling on the western sides of islands, primarily Fernandina, Isabela, and Floreana Islands. Warm, subtropical water flows into the archipelago from the northeast via the Panamá current, primarily affecting the northern (Wolf and Darwin) and central (Pinta, Marchena, and Genovesa) islands. These currents are seasonally variable, depend on the intensity of trade winds, and are indirectly influenced through Pacific basin atmospheric pressure differentials, including significant effects from ENSO. Overall, compared to other equatorial marine habitats, sea surface temperatures are relatively cool in the eastern equatorial Pacific (Chavez and Brusca 1991). Overlaying this general trend are periods of anomalously warm and cool sea surface temperatures associated with the warm and cool phases of ENSO (El Niño and La Niña, respectively) (Feingold 2011).

This complex water mass mixing creates patterns of distinct coastal, benthic environmental zones as identified by Glynn and Wellington (1983). Macrophytic algal communities occur on the western coastlines of Fernandina, Isabela, Floreana, Española, and San Cristobal Islands, and conditions conducive to coral development are present on most eastern and northern coasts of these and other large islands, including Santiago, Pinta, Marchena, Genovesa, Santa Cruz, Santa Fe, and Española. Coastlines with southeastern exposures remain relatively unsurveyed due to high wave energy and surge. Notable exceptions to this general trend occur along the east coast of Fernandina and west coast of Isabela, areas in the protected waters of the Bolivar Channel. Microhabitats in relatively warm, shallow embayments and subtidal lava pools are conducive to coral growth even though surrounding colder and deeper waters are not. Dawson et al. (2009b) developed a habitat suitability model based on sea surface temperature data to document likely locations of coral presence in the archipelago.

The most northerly islands of Wolf and Darwin experience much different environmental conditions than the remainder of the archipelago and support the best developed coral formations. Wolf is 140 km distant from its nearest southern neighbors of Isabela and Pinta, and Darwin is 35 km further north. Their location to the northwest of the main archipelago places these barely emergent oceanic pinnacles in relatively warm, subtropical waters bathed seasonally (January–April) by the Panamá current. Well-developed coral communities and marginal reefs, composed primarily of *Porites lobata*, occur on the east/northeast sectors of these islands in 3–20 m depths.

El Niño-Southern Oscillation (ENSO) results from a wide-scale shift in pressure centers related to feedback cycles within the coupled ocean-atmosphere climate

system of the tropical Pacific, potentially influenced by external forcing (Enfield 1989). This causes environmental perturbations across the entire region, with particularly strong effects centered in the east Pacific where the Galápagos Archipelago is located. Very strong events are relatively uncommon; however, two El Niño disturbances of this magnitude occurred within two decades, the 1982–1983 and 1997–1998 events. The most debilitating impacts to corals result from seawater temperature anomalies. Persistent (weeks to months) elevation of temperatures that are only 1–2 °C above long-term means can result in coral bleaching (loss of zooxanthellae endosymbionts and/or their photosynthetic pigments) and mortality (Robinson 1985; Glynn and D’Croz 1990).

Coral Reefs and Coral Communities

Scleractinian corals are calcium carbonate-secreting cnidarians that exist as individuals (single polyps, e.g., *Diastrea*) or form colonies of multiple polyps (e.g., *Pocillopora* and *Porites*). Colonial corals may attain large size (several meters in diameter) through asexual reproduction of polyps and may live hundreds of years. Some colonial species create the main structure of coral reefs and are called hermatypic (reef-building) corals (e.g., *Pavona* and *Porites*). Ahermatypic corals do not substantively contribute to reef structure but may be present as isolated individuals or colonies on hard substrata and as minor components on coral reefs or on unconsolidated sediments. Hermatypic corals are zooxanthellate, that is, they possess endosymbiotic dinoflagellates within their gastrodermal tissues. Zooxanthellae contribute significantly to coral energy needs and enable increased carbonate secretion rates compared to azooxanthellate species. Azooxanthellate species (e.g., *Tubastraea*) are not hermatypic since they do not form reef structure (see below for definition of “coral reef”). However, some ahermatypic corals are also zooxanthellate; they also do not form reef framework even though they possess zooxanthellae (e.g., *Psammocora*).

The term “coral reef” has been utilized in various ways, especially during the past few decades, to include any benthic community with coral as an important structural component. This broad definition includes bioherms (mounded, loose carbonate sediments) formed by corals on unconsolidated substrata and in areas beneath the photic zone. In this contribution, the term “coral reef” is used to denote a structural formation in the photic zone; “if coral populations continue to build upon products of their own making, they are termed structural reefs (true coral reefs); and, if not, they are defined as coral communities” (Glynn and Wellington 1983). Further, this definition requires the accretion of carbonate material vertically towards the sea surface and distinguishes true coral reefs from the way corals are more typically encountered in the archipelago, namely, as widely scattered colonies on basalt substrata. Under these definitions, coral reefs are no longer present in the main part of the archipelago (southern and central islands), with marginal reef development still present at the northern islands of Wolf and Darwin. Specifically, the coral reefs reported by Glynn and Wellington (1983) in the main archipelago

Fig. 1.1 Large *Porites lobata* colony at Wolf Island (11 m depth, June 2012). Measuring stick near the top of the colony is 1 m long



(e.g., Devil’s Crown) have mostly disappeared following the 1982–1983 El Niño disturbance. Remaining relict structures are composed of degraded coral skeletons without contributions of living corals to carbonate framework production. Corals at the northern islands have maintained marginal coral reef status with up to 3.5 m of carbonate accretion above their basalt base (Fig. 1.1). The base of another sampled large *Porites* tower from Darwin Island was ^{14}C dated to approximately 500 years, indicating several centuries of growth at this location.

According to Wells (*In: Glynn and Wellington 1983*), there were approximately 13 species of hermatypic (reef-building) scleractinian corals and 31 species of ahermatypes reported from the Galápagos Islands. Hickman (2008) reported 22 species of hermatypic corals, including 9 species of *Pocillopora*, though using a broader definition of “hermatypic” than in this chapter. These numbers vary with advances in coral taxonomy and, after a period of increase, are now poised to decrease with the possible consolidation of species in the genus *Pocillopora*. Morphologically variable forms in this genus that are now considered different species may not be as genetically distinct as once recognized (Pinzon et al. 2013). Only a few species of hermatypic coral are common components of coral communities in the archipelago. These same few species may form structural reefs throughout the eastern tropical Pacific region and include *Pocillopora* spp., *Pavona clavus*, *Pavona gigantea*, and *Porites lobata* (Glynn and Wellington 1983; Glynn and Ault 2000). In addition, several species that form non-reefal carbonate accumulations contribute to coral species diversity and ecologically important communities that are more structurally complex than adjacent sand and rubble benthic habitats. Examples include free-living forms such as the fungiid *Diaseris distorta* and a branching morphotype of *Psammocora stellata* (Feingold 1996). Also, the ahermatypic (non-reef-forming) orange cup coral *Tubastraea coccinea* is an important component of rocky outcrops and vertical walls where it competes for space with other sessile benthic invertebrates such as sponges, barnacles, and ascidians (Witman and Smith 2003). Numerous species of other azooxanthellate, ahermatypic corals are found under ledges, in other cryptic habitats, and at greater depths (Wells *In: Glynn and Wellington 1983*).

Coral Research: A Historical Sketch

According to Darwin (1842), there were no coral reefs in the eastern tropical Pacific, and he made only a few brief references to Galápagos corals during his celebrated visit to the archipelago in 1835 aboard the HMS Beagle (Wells *In*: Glynn and Wellington 1983). Benthic marine organisms were not a focus of his studies and were difficult to observe due to technological limitations to underwater operations that persisted until the latter half of the twentieth century.

Early scientific expeditions to Galápagos did expand our knowledge of corals, and collections made during cruises of the HMS Beagle (1835), R/V Hassler (1872), and R/V Albatross (1888) included about 15 species of corals and the discovery that coral debris contributed importantly to beach sediments in the archipelago (Glynn and Wellington 1983).

A series of scientific expeditions, financed by Allan Hancock, significantly increased existing knowledge of marine organisms in the Galápagos Islands. The voyages of Oaxaca (1928) and Velero III (1931–1938) brought researchers to the archipelago who collected material that formed the basis of a systematic revision of eastern Pacific corals. Durham and Barnard (1952) published additional information on Galápagos corals as part of the Galápagos International Scientific Project.

Following this era of taxonomic cataloging of coral species, attention turned to their ecological role in shallow, nearshore habitats. Coral reefs are widely distributed in the eastern tropical Pacific and are all fringing or patch reefs that grow in shallow shelf waters on suitable substrata (Cortés 2011); however, reef development was and remains limited in the Galápagos Islands. Nevertheless, these low-diversity Galápagos coral communities still increase benthic structural complexity and create carbonate substrata that can be utilized by numerous other organisms. For example, excavating marine mollusks (*Lithophaga* spp.) construct tunnels in massive corals such as *Porites lobata*. Numerous apertures for their siphons can be observed as hourglass-shaped openings among coral polyps. Echinoids such as *Eucidaris*, *Tripneustes*, and *Diadema* shelter within crevices that they themselves may construct. Furthermore, in the first ecological paper on Galápagos coral reefs, Glynn et al. (1979) observed that the endemic echinoid *Eucidaris galapagensis* degraded existing reef structure and interfered with the establishment of new reef frameworks in the archipelago. This sea urchin species was identified as *E. galapagensis* (Lessios et al. 1999) after publication of the 1979 study where it was referred to as *E. thouarsii*. Part of the reason that this distinction was made was because *E. thouarsii* does not have the same bioerosive effects on the mainland or other eastern Pacific locations as does *E. galapagensis* in the archipelago. Coral-associated fish species shelter among the colonies, and several opportunistic coral browsers such as parrotfish and Moorish idols utilize coral as important dietary supplements. Damselfishes, primarily *Stegastes arcifrons*, create algal gardens adjacent to and often encroaching on coral colonies (Fig. 1.2). They are common within aggregations of *Pocillopora* and *Porites*. The obligate corallivorous puffer

Fig. 1.2 Damsel fish (*Stegastes arcifrons*) algal lawn adjacent to a *Pocillopora* sp. colony, Concha y Perla lagoon, Isabela Island (2 m depth, June 2012). Note truncated coral branch tips at base and periphery of colony due to biting by the damselfish



fish *Arothron meleagris* is often seen associating with the corals and has particularly high abundances on the *Porites* reefs at Wolf and Darwin Islands.

One benefit to corals in Galápagos is the near absence of the predatory sea star *Acanthaster planci*. This destructive corallivore has been observed on only a few occasions on corals at Wolf and Darwin Islands but never in the central and southern archipelago. Perhaps food resources are too meager, or the relatively cool water does not allow larval development and/or settlement. *Acanthaster* feeding behavior in other parts of the eastern tropical Pacific has resulted in serious impacts to targeted coral prey species (Glynn 2004).

Galápagos coral reefs and coral communities were first documented in detail in the 1970s by Wellington who described reef structures from Devil's Crown and Champion Island, two islets off the north coast of Floreana Island. Wellington (1975) then produced the first broad-based report of marine resources, including corals, for the nascent Galápagos Marine Reserve. Later, more comprehensive studies by Glynn and Wellington (1983) provided archipelago-wide information for Galápagos coral researchers. Their book, *Corals and Coral Reefs of the Galápagos Islands*, documented in detail the distribution and abundance of scleractinian corals throughout the archipelago. This work was fortuitously completed immediately prior to the 1982–1983 El Niño warming disturbance. Since that disturbance event nearly eliminated corals from ecologically meaningful roles throughout the south-central parts of the archipelago, this information now serves as a valuable baseline for contemporary studies. More recently, a summary of the condition and distribution of coral reefs and coral communities in Ecuador was reported by Glynn (2003).

Tectonic uplift is an unusual type of disturbance to corals associated with areas subject to active volcanism such as the Galápagos Archipelago. Colgan and Malmquist (1987) reported on the uplift and subaerial exposure of the nearshore coral community at Urvina Bay, Isabela Island (Fig. 1.3). This event occurred in 1954, and the seafloor was elevated nearly 6 m, exposing an area of several square kilometers. Clearly, subaerial exposure results in the rapid mortality of corals, but even those colonies that were simply raised into shallow water were likely affected.

Fig. 1.3 Uplifted *Pavona clavus* colony (approximately 2 m diameter), Urvina Bay, Isabela Island (June 2012)



The shoaling of the shoreline affected these barely submerged colonies by exposing them to higher solar radiation stress and increased wave energy. Despite the cool conditions in this region of the archipelago, a robust coral community developed in Urvina Bay. One of the uplifted coral colonies (*Pavona clavus*) was approximately 5 m in diameter and dated to 347 years based on annual skeletal density bands and radiometric dating (Dunbar et al. 1994).

Research through the 1980s and 1990s focused on ENSO impacts, primarily the effects of elevated water temperatures (Glynn and D’Croz 1990), on these degraded coral communities. Two strong El Niño warming events (1982–1983 and 1997–1998), one in each of these decades, sparked research in the Galápagos as part of a wider effort throughout the eastern tropical Pacific region. Robinson and del Pino edited a volume on the impacts of the 1982–1983 ENSO to Galápagos organisms, including a chapter (Robinson 1985) on marine life that reported coral bleaching and mortality at known reef sites at Devil’s Crown and Champion Island. In addition, there was concern about the possible extinction of the endemic cup coral *Tubastraea tagusensis*. Populations recovered in Tagus Cove on the west coast of Isabela Island, and the species may have recently been introduced to Brazil (Creed 2006; Hickman 2008). However, its congener *Tubastraea floreana* remains on the IUCN red list as critically endangered, with distribution restricted to Cousin’s Rock, Santiago, and Isla Gardner, at Floreana Island. Two book volumes edited by Glynn (1990, 2001) contain contributions that elucidated the impacts and longer term consequences of ENSO activity on corals. Studies of this natural phenomenon focused on its effect on coral physiology, ecology, reproduction, and distribution. Also, during this time, the work of international scientists became supplemented and augmented by surveys and monitoring projects at the Charles Darwin Research Station and Galápagos National Park Service. In particular, research by Edgar et al. (2008) identified key threatened marine species in the Galápagos Marine Reserve, including corals. The protection of key biodiversity areas was also proposed. Later, Edgar et al. (2010) documented major ecological phase shifts as a consequence of ENSO impacts through a comparison of historical and contemporary datasets for shallow reef habitats. Seven coral species were recognized as

globally threatened, including two species of the important reef-building coral *Pocillopora*. The remaining five species (*Rhizopsammia wellingtoni*, *T. floreana*, *Polycyathus isabela*, *Fungia curvata* (*Cycloseris curvata*), and *Psammocora stellata*) are not structural components of reefs, but nonetheless contribute to ecosystem complexity and benthic structural heterogeneity. Banks et al. (2009) documented the status of reefs at Wolf and Darwin and suggested the implementation of a mooring buoy system to mitigate impacts associated with tourist diving activities.

A recent interesting line of research is focusing on thermal tolerance differences among different clades of the photosynthetic dinoflagellate coral endosymbiont *Symbiodinium*. Baker (2003) reported that different clades of zooxanthellae have differing tolerances to temperature and light levels and distinct photosynthetic efficiencies. Thus, corals that survived the 1982–1983 El Niño were preadapted to survive similar conditions associated with the subsequent 1997–1998 El Niño event. In Galápagos, Glynn et al. (2001) reported only 26.2 % mortality following the 1997–1998 El Niño, compared to 95–99 % mortality associated with disturbances from the 1982–1983 El Niño. Corals with multiple clades in their tissues can benefit from having symbionts that function effectively under a variety of conditions, including seawater warming. However, this form of bet-hedging comes with the price of reduced efficiency (e.g., growth and competitive ability) when conditions are less extreme.

A series of studies dealing with coral reproduction in the Galápagos Islands, and the eastern tropical Pacific, documented high levels of gamete output (fecundity) from sexual reproduction, but with low levels of recruitment. Despite resultant reductions in genetic diversity, the relative importance of asexual reproduction for maintenance of local Galápagos coral populations was emphasized (Glynn et al. 1991, 1994, 2011, 2012). Regarding sexual reproduction, gamete spawning was only observed in the field over a single 2-day period in several colonies of *Pavona gigantea* at Devil's Crown. However, histological examination of collected specimens documented that most species produce mature eggs and sperm that are presumably spawned. No gamete reabsorption has been observed. Asexual reproduction (fragmentation) is a particularly important mode for branching corals such as *Pocillopora* spp. and *Psammocora stellata* and for the brittle fungiid coral *Diaseris distorta*. Though most fragmentation is induced by mechanical stress from external physical forces such as waves and current, *Diaseris* is capable of performing autotomy, a process by which the coral can divide through selective dissolution of skeletal components (Yamashiro and Nishihira 1998; Colley et al. 2002).

Although most of the research on Galápagos corals has focused on reef-building species, there are two free-living (unattached) species that form ecologically significant aggregations that create low-relief three-dimensional structures on sand and rubble substrata. These include *Psammocora stellata*, a small, branching colonial coral, and individuals of the fungiid (mushroom) coral *Diaseris distorta*. *Psammocora* is widespread in the archipelago and can be found adjacent to and intermingled with reef-building species. Its ability to tolerate water motion and high

sediment loads allows it to survive in suboptimal coral habitats. Temperature tolerance experiments documented that it is more resistant to bleaching than other Galápagos corals (Feingold 1995). Its designation as threatened (Edgar et al. 2010) in the archipelago may be premature as several impacted populations have recently recovered to near pre-disturbance levels. Also, this species has been observed in a wide variety of habitats (1–30 m depths) throughout the archipelago, perhaps more so than any other Galápagos coral species.

Living populations of the fungiid coral *Diaseris distorta* are known from only one location in the Galápagos Islands, east/northeast of Devil's Crown (Fig. 1.4). Populations can exceed 100 % live cover due to stacking and overlap among individuals. These corals are distributed over a sandy bottom area, also containing rocky basalt outcrops, approximately 1 km² in depths between 12 and 34 m. The population was estimated in the 100 s of thousands of individuals (Feingold 1996), but their restriction to one location within the archipelago places them at risk. The ability of this species to auto-fragment allows great potential for population growth through asexual reproduction (Colley et al. 2002). Hundreds of dead skeletons of *Diaseris* were also observed at 11–13 m depth near Xarifa Island in Gardner Bay, Española Island, but despite extensive searches along the adjacent coastline, no living specimens were found. Associated with this coral at Devil's Crown is another fungiid, *Cycloseris elegans*, but populations are much smaller, with less than 100 individuals present in 2012. Like *Diaseris*, dead skeletons of *Cycloseris* were observed near Xarifa Island in Gardner Bay, Española Island, and at relatively high densities. Dead skeletons of *Cycloseris* were also recently (2012) observed at Darwin Island at the base of a poritid reef at 25–30 m depths. This confirms their presence at other locations in the past, but this species is now known from only a single location in a critically small population. Tourists who plan to scuba dive in their habitat at Devil's Crown should be briefed on the threatened status of this species.

In the early twenty-first century, coral scientists participated in a series of cruises supported by the Darwin Initiative Project, sponsored by the government of the United Kingdom through the Department for Environment, Food, and Rural Affairs (DEFRA), culminating in a special issue of Galápagos Research (Dawson et al. 2009a). The authors noted that “The coral reefs of the Galápagos Islands contribute significantly to species richness and diversity in the Galápagos Marine Reserve (GMR)” and that these communities were impacted by climatic disturbances, most notably El Niño-Southern Oscillation.

New scleractinian coral species and records were reported during the Darwin Initiative cruises, including *Pocillopora effusus*, *Pocillopora inflata*, *Pavona chiriquiensis*, and *Leptoseris* sp. (Dawson et al. 2009a). However, recent genetic analyses determined that many species in the eastern Pacific *Pocillopora* clade, including those in the Galápagos Islands, may be morphological variants rather than distinct species (Pinzon et al. 2013). Additionally, molecular genetic evidence suggests that a second species of Poritidae may be present in the archipelago, *Porites evermanni* (Baums, personal communication). The dynamic nature of scientific inquiry, particularly taxonomic revisions, will continue to expand and improve our knowledge base of these important marine cnidarians.

Fig. 1.4 *Diaseris distorta* individuals at Devil's Crown, Floreana Island (15 m depth, June 2005). Polyps were 3–5 cm in diameter



Resilience and recovery of coral populations from ENSO disturbances are themes of recent research and were reported from several locations in the archipelago, most notably the northern Islands of Wolf and Darwin (Glynn and Ault 2000). Recovery was poor elsewhere, with most species maintaining a presence in their respective environments but at low population densities. Glynn et al. (2009) reported that coral reefs in the northern islands of Wolf and Darwin demonstrated significant recovery since experiencing impacts from the 1982–1983 El Niño. In particular, the sections of reef dominated by massive colonies of *Porites lobata* displayed live coral cover exceeding 20 %. In 2007, overall live coral cover on Darwin reef was 21.1 % and 32.3 % in 2012. This increase in coral cover of 53.1 % indicates that recovery is occurring in the area. *Pocillopora* spp. were present on these reefs of the northern islands, though not nearly in the same abundance as before the disturbance. Recent surveys performed by Glynn, Riegl, and Feingold in June 2012 corroborated these observations. Despite focused searches at locations where *Pocillopora* previously (pre-1982–1983 El Niño) formed extensive monospecific stands, no section of the reef was primarily composed of *Pocillopora*. During these surveys, one colony was observed at 28 m depth, greatly below the typical depth for this phototrophic species. In the southern part of the archipelago, Paul (2012) documented decline and recovery of *Porites lobata* at Devil's Crown, Floreana Island, following the 1997–1998 El Niño. From a broader perspective, live *Porites* total tissue area increased from $5.80 \pm 2.3 \text{ m}^2$ in 1993 to $6.92 \pm 3.4 \text{ m}^2$ in 2011 ($n = 10$ colonies). This was an average increase of 16.2 %; however, the difference was not statistically significant.

A comprehensive study by Edgar et al. (2008) investigated key biodiversity areas (KBAs) and identified marine habitats important in coral conservation and management within the Galápagos Marine Reserve. They noted that two coral species are listed on the 2006 International Union for Conservation of Nature and Natural Resources (IUCN) Red List of threatened species and bear special protection. These included the ahermatypic corals *Rhizopsammia wellingtoni* and *Tubastraea floreana*.

Fig. 1.5 Aggregation of *Pocillopora* sp. at Concha y Perla lagoon, Puerto Villamil, Isabela Island (2 m depth, May 2013). Measuring stick is 1 m long



During a recent research cruise to the archipelago (June 2012), an aggregation of *Pocillopora* sp. (c.f. *damicornis*) was surveyed within the shallow (2–3 m depth) Concha y Perla lava pools at Puerto Villamil, Isabela Island (Fig. 1.5). This previously undocumented population now represents the largest known aggregation with the highest percent cover of this genus within the archipelago. Approximately 1,600 colonies were observed. Total live tissue area was 40.3 m², with a mean colony surface area of 248 cm². Genetic analysis documented that all of these colonies are a single genet (Baums, personal communication), i.e., they are all members of a single clone. This underlines the importance of asexual reproduction of *Pocillopora* in the Galápagos Islands.

Responses of Corals to Broad-Scale Impacts

Global climate change and associated sea surface warming and ocean acidification are drivers of significant disturbance to corals (Hoegh-Guldberg et al. 2007). Anomalously warm or cool water temperatures cause coral bleaching, the loss of endosymbiotic dinoflagellates (zooxanthellae), with particularly dire results in the Galápagos Archipelago. Since zooxanthellae produce a significant share of the energy requirements of hermatypic (reef-building) corals, their extended presence in low numbers or significant photosynthetic pigment loss during bleaching (Fig. 1.6) resulted in mortalities of 95–99 % following the 1982–1983 El Niño, a particularly severe event (Glynn 1990). As the atmospheric concentration of CO₂ increases, its diffusion into oceanic surface waters results in decreased pH. This ocean acidification lowers carbonate saturation states, making calcium carbonate precipitation more difficult and resulting specifically in decreased coral skeleton density. Since the pool of oceanic water around the Galápagos Islands has considerably lower pH than the rest of the eastern tropical Pacific, the corals living there may be particularly at risk should acidification continue to increase. Also, Galápagos corals may serve as

Fig. 1.6 Coral bleaching at Punta Espejo, Marchena Island, during the 1997–1998 El Niño warming event (7 m depth, March 1998). Bleached colonies of *Pavona clavus* are behind bleached and pale colonies of *Porites lobata*, foreground



contemporary harbingers of forthcoming disturbances to other coral environments (Manzello et al. 2008).

Although there is controversy surrounding the linkage between warming associated with climate change and the increased frequency and intensity of ENSO events (Stot et al. 2000; Enfield 2003), two severe events in two decades (1982–1983 and 1997–1998) impacted Galápagos corals. Baker et al. (2008) reported that continued ecological function of these coral ecosystems is in jeopardy due to several factors. These include (a) degree of coral cover loss, (b) challenges associated with acclimatization of surviving species to higher temperatures, (c) maintenance of carbonate structures as a balance between accretion and erosion, and (d) maintenance of resiliency. Resiliency, however, should be less of a problem in the Galápagos Islands compared to other eastern Pacific regions since overfishing of important reef herbivores (fishes and sea urchins) is greatly reduced. By contrast, Edgar et al. (2010) noted that the removal of lobsters and large fish predators magnifies the impacts of ENSO through trophic cascades. In their analysis, they noted that coral cover increases with distance from fishing ports, providing evidence of third-order trophic effects. The overfishing of large predators and resultant “release” of their prey species increase benthic grazing pressure in heavily fished areas. Of particular concern is the persistent large populations of the pencil sea urchin *Eucidaris galapagensis* that may prevent coral settlement and recruitment due to their grazing activities on the benthic substrata (Glynn 1988).

Disturbance by aperiodic ENSO events regularly exceeds the physiological thermal tolerance limits of corals in the Galápagos Islands, contributing to the creation of a marginal habitat for coral survival. These events affect corals and numerous other marine organisms, with anomalously elevated water temperatures during warm-phase (El Niño) and anomalously depressed water temperatures during cool-phase (La Niña) periods (Feingold 2011). Elevated temperatures were associated with bleaching and high mortality (95–99 %) of corals in the archipelago during the very strong 1982–1983 event (Glynn et al. 1988), resulting

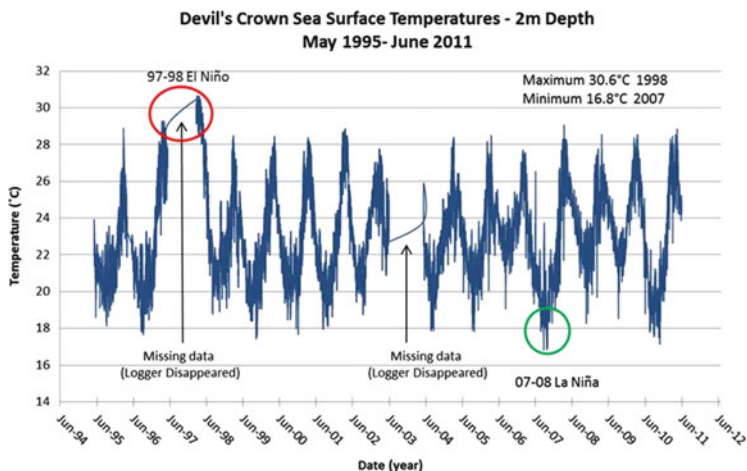


Fig. 1.7 Sixteen years (1995–2011) of in situ seawater temperature data, 2 m depth inside Devil’s Crown, Floreana Island. Values were obtained at 30-min or hourly intervals with Onset Instrument submersible data loggers. Note ENSO-related warm (1998 El Niño) and cool (2007 La Niña) conditions

in dramatic losses of coral cover and species diversity (Glynn 1990). Cool conditions in 2007 (Fig. 1.7) also resulted in coral bleaching and mortality in the Galápagos Archipelago (Banks et al. 2009) and at other eastern Pacific locations (Reyes-Bonilla et al. 2002). This La Niña cooling was associated with dramatic losses (95 %) in a recovering *Pocillopora* spp. coral population at Devil’s Crown, Floreana Island. However, Paul (2012) reported live tissue cover increases for *Porites lobata* at the same site and depth (Devil’s Crown) during extreme cooling associated with the 2007–2008 La Niña event.

ENSO-related coral bleaching occurs when endosymbiotic dinoflagellates (zooxanthellae) either diminish in number within the coral host tissues or lose their photosynthetic pigments. Since zooxanthellae are an important source of metabolic energy, reef-building corals will die unless sufficient populations of the endosymbiont become reestablished when conditions normalize. For example, reef-building species such as *Pavona clavus* can survive up to 60-day periods of bleaching (Feingold 2001); however, the ahermatypic fungiid *Diaseis* can survive in the bleached state for over 180 days (Feingold 1996), perhaps due to its ability to effectively feed heterotrophically (e.g., by ingesting zooplankton). Bleaching severity shows species-specific trends, with some corals being sensitive, bleaching sooner and more completely (e.g., *Pocillopora*) than other more resistant species (e.g., *Psammocora* and *Porites*) (Robinson 1985; Glynn 1990; Feingold 1995). Bleaching occurs when coral is physiologically stressed and is most often associated with positive SST anomalies (warming), although other perturbations such as cooling, lower sea level leading to emersion, salinity decrease, and sedimentation contribute to this stress response.

Bleaching sensitivity is also related to the endosymbiont clade; some zooxanthellae are more tolerant of elevated temperatures than others. For example, in Panama pocilloporid corals with zooxanthellae in clade D did not bleach during the 1997–1998 El Niño event, whereas those with clade C endosymbionts did bleach (Baker 2004). Thus, coral survivors of the 1982–1983 El Niño likely harbored clade D endosymbionts, and when these corals were exposed to highly elevated temperatures again in 1997–1998, they were not so severely affected (Glynn et al. 2001).

Of particular concern to the recovery of coral communities in the Galápagos is the secondary loss of carbonate substrata following coral mortality. This region of the eastern tropical Pacific has much lower pH values (7.88) than the rest of the region that typically exceeds pH values of 8.00. Lower pH causes depressed aragonite saturation levels of 2.49 compared with more typical values of ~3.80 for the tropical surface ocean (Manzello et al. 2008). This results in lower coral skeletal densities than usual, and weak subsequent cementation exacerbates the effects of echinoid bioerosion that typically follows coral mortality (Glynn 1988). Manzello et al. (2008) suggested that skeletal deposition by corals in the Galápagos Islands could thereby serve as a model for other areas of the world at elevated atmospheric CO₂ levels approximately double current values.

Carbonate bioerosion rates in the Galápagos Islands (average of 25.4 kg CaCO₃ m⁻² year⁻¹) are among the highest known in the eastern tropical Pacific region (Reaka-Kudla et al. 1996) and are two orders of magnitude higher than values reported from the Caribbean. Glynn et al. (1988) documented extensive destruction of the reef formed by the branching pocilloporid corals at Devil's Crown by *Eucidaris galapagensis* (= *E. thouarsii*) following the 1982–1983 El Niño. This species of sea urchin is a significant bioeroder where it occurs in the Galápagos Islands (Glynn et al. 1979) and at Cocos Island; *Diadema mexicanum* fulfills this role in other parts of the eastern tropical Pacific (Glynn 1988). The pocilloporid framework at Devil's Crown was completely degraded in the following post-bleaching decade from continued grazing of *Eucidaris* that reduced the 1–2 m thick carbonate framework to rubble and sand. Coral colony erosion and loss were also reported for massive species at other locations throughout the archipelago. Several observations documented this destructive process. For example, (a) *Porites lobata* colonies became mushroom shaped from basal bioerosion at Bartolomé Island 6 years after disturbance, (b) a 2 m diameter colony of *Pavona gigantea* collapsed and tumbled downslope from 3 to 32 m depth at Champion Island approximately 10 years after disturbance, and (c) a large *Porites lobata* colony in the anchorage at Santa Fe Island was reduced to rubble during the two decades after colony mortality.

Following these types of disturbances, coral recovery relies on two important reproductive modes, sexual reproduction via planula larvae and asexual reproduction. Asexual reproduction involves two basic processes (a) replication of polyps allowing colony growth and recovery from partial damage through the re-sheeting of surviving colony tissues and (b) fragmentation that allows coral replication through physical or biological processes. Sexual reproduction is important in dispersal and promoting genetic diversity, while asexual reproduction maintains

genotypes that were capable of surviving under local conditions, including ENSO disturbances (Colley et al. 2006).

In addition to coral bleaching and mortality, ENSO can have sublethal effects on corals that affect their ability to persist and colonize new habitats in the archipelago. Reproductive activity (gametogenesis) in some important reef-building corals (e.g., members of the Pocilloporidae, Poritidae, and Agariciidae) can be either detrimentally affected or enhanced by El Niño-related seawater warming. Moderate to weak events can improve conditions for reproductive success since reproduction typically occurs under warmer conditions; however, strong events can cause reproductive failure if temperatures increase too rapidly or rise too high (Colley et al. 2006). Some evidence suggests that corals disperse to the tropical eastern Pacific via countercurrents that transport water from the west to the east. During an ENSO warm phase, the velocity and volume flow of these currents increase allowing the more rapid transport of larvae and improved chances for dispersion and recruitment of corals originating in the central Pacific to the eastern Pacific (Glynn and Ault 2000). Also, reproductively active corals on the Ecuadorean mainland (e.g., in the Machalilla National Park) could release larvae capable of traveling to the Galápagos Archipelago, particularly when the Panamá current is seasonally strong (January–April). Upstream conservation of corals, through the use of marine protected areas (MPAs), potentially increases the resiliency of corals in the archipelago.

Anthropogenic Stress on Galápagos Corals

Compared to most other regions in the eastern tropical Pacific, and even globally, there is less direct anthropogenic impact to corals in the Galápagos Islands. This is due to several factors (a) the relatively small human populations on only 4 of the 13 larger islands, (b) the lack of any human habitation in the central and northern archipelago where coral development is most robust, and (c) limited direct extractive use of scleractinian coral community resources. According to Glynn (1994), natural disturbances such as strong ENSO events are of greater concern than anthropogenic impacts. However, anchor damage, extraction of corals (particularly *Pocillopora*) for use as curios, and mechanical damage to corals from fishing activities were mentioned. Also, extractive fisheries have been associated with reduced coral cover and a variety of other ecological perturbations due to trophic cascades (Edgar et al. 2010). The use of marine protected areas (MPAs) was invoked as a mechanism to ameliorate these anthropogenic perturbations. Of greater concern are impacts associated with anthropogenically accelerated climate change, including sea surface warming and ocean acidification. These are broader scale impacts addressed in an earlier section of this chapter and require multinational, comprehensive solutions. In the habitat suitability model proposed by Dawson et al. (2009b), a predictive element is incorporated that takes into account global climate change.

Since corals are generally found as colonies scattered over large areas in the Galápagos Islands, specific recommendations for management must be focused on the few locations with abundant coral cover. The northern islands of Wolf and Darwin are remote, helping to reduce impacts on the *Porites* reefs along the shelves of their respective shorelines. However, increased visitation by divers and continued poaching of fishes (particularly sharks) jeopardize trophic system balance. It is recommended that fisheries bans within the Marine Reserve are rigorously enforced and that the well-regulated tourism is augmented with specific mention of the sensitive nature of Galápagos corals. As suggested by Banks et al. (2009), a system of mooring buoys would mitigate impacts by boat operations associated with tourist diving activities, particularly anchor damage. Dive sites are accessed by small boats that do not anchor (live boating), so the primary concern is with the live-aboard vessels that transport tourists from island to island. Protocols were suggested by Merlen et al. (2009) for mooring buoy deployment throughout the archipelago, and they are now in place at Bartolomé Island and Punta Cormorant, Floreana Island. Moorings at additional locations would provide further benefit, particularly at the northern islands of Wolf and Darwin where anchoring is difficult due to the steep shelf slope.

Corals present at Devil's Crown, Floreana Island, include approximately 30 large (0.5–1.0 m diameter) colonies of *Porites lobata* that survived and recovered from the 1982–1983 El Niño (Fig. 1.8). Nevertheless, these corals experienced a period of live tissue decline following the 1997–1998 El Niño and then showed recovery from 2000 to 2009 (Paul 2012). Also, there are now approximately 20 colonies of *Pocillopora* spp. within Devil's Crown, a location that formerly supported (prior to the 1982–1983 El Niño) an extensive pocilloporid coral reef consisting of thousands of colonies. Following the loss of this reef in the decade following the El Niño event, this population had partially recovered to 167 colonies but underwent decline between 2007 and 2009, likely associated with cool water impacts of the 2007 La Niña event. Banks et al. (2009) reported archipelago-wide bleaching of *Porites lobata* and *Pocillopora* sp. during this period, attributed to “cold shock.” Another example of recovery within Devil's Crown concerns a population of *Psammocora stellata* that decreased from nearly 100 % cover in the 1970s to widely scattered colonies following the 1982–1983 ENSO and has now nearly fully recovered (Fig. 1.9). The interior of Devil's Crown is now closed to tourist activities, and this is expected to aid continued recovery by minimizing human impacts. When the area was open in the past, snorkelers were observed standing on coral colonies and causing direct mechanical damage to coral tissues. In addition, sediments resuspended by snorkeler's swim fins settled on horizontal coral colony surfaces. This increased sedimentation stresses corals that must expend metabolic energy to remove the particles. Now that these avoidable stressors have been eliminated, hopefully this will improve coral settlement and recovery. It is heartening news that two (*Porites* and *Psammocora*) of the three monitored coral species that were present at Devil's Crown prior to the 1982–1983 ENSO have recovered.

Corals at the sites of two other former reefs (Champion Island, near Floreana Island, and the lava pools at Punta Espinosa, Fernandina Island) have not fared

Fig. 1.8 Colonies of *Porites lobata* (2 m depth, June 2011) form an aggregation in the submerged caldera of Devil's Crown, Floreana Island. The colony in the foreground is approximately 1 m in diameter



Fig. 1.9 Colonies of *Psammocora stellata* inside Devil's Crown, Floreana Island (3 m depth, June 2007), recovered from impacts associated with 1982–1983 El Niño warming to nearly the same density and distribution as before the event. The largest colonies are approximately 10 cm in diameter



as well. Surveys at Champion Island were performed annually or biannually since the early 1990s. Continued bioerosion eliminated most of the carbonate substrata, predominantly composed of *Pavona clavus* skeletal material. As in other parts of the archipelago, scattered coral colonies are still present, but there are no longer sufficient numbers or densities of colonies to form reef frameworks. A survey of the lava pools at Punta Espinosa in 2002 revealed intact dead skeletons of *Pocillopora* still in growth position, but no living colonies or new coral recruits.

The location of a dense population of *Pocillopora* colonies in Concha y Perla lagoon, so close (~1 km) to a town center (Puerto Villamil, Isabela Island), provides an exceptional opportunity for education and ecotourism. However, their unique genetics (all one genet that is not found elsewhere in the archipelago) (Baums, personal communication) and concerns of potential human impacts mandate their protection. The touristic appeal of these corals, combined with their delicate status in the archipelago, signifies that they are a population of special concern. It is recommended that programs be established to educate the local population and

visitors of this unique and sensitive resource. Every effort should be made to prevent any type of anthropogenic insult, such as septic tank leakage or extractive activities, while encouraging its use in local education.

In summary, corals in the Galápagos Islands persist despite experiencing environmentally marginal conditions that are associated with the general cool conditions of the region, and that are punctuated by aperiodic anomalously warm and cool water stressors associated with ENSO activity. The study of these intriguing organisms at the physiological limits of their distribution provides meaningful insights into future challenges faced by corals in a changing world.

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