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State of corals and coral reefs of the Galápagos Islands (Ecuador): Past, present and future[☆]

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ABSTRACT

Coral populations and structural coral reefs have undergone severe reductions and losses respectively over large parts of the Galápagos Islands during and following the 1982–83 El Niño event. Coral tissue loss amounted to 95% across the Archipelago. Also at that time, all coral reefs in the central and southern islands disappeared following severe degradation and eventual collapse due primarily to intense bioerosion and low recruitment. Six sites in the southern islands have demonstrated low to moderate coral community (scattered colonies, but no carbonate framework) recovery. The iconic pocilloporid reef at Devil's Crown (Floreana Island) experienced recovery to 2007, then severe mortality during a La Niña cooling event, and is again (as of 2017) undergoing rapid recovery. Notable recovery has occurred at the central (Marchena) and northern islands (Darwin and Wolf). Of the 17 structural reefs first observed in the mid-1970s, the single surviving reef (Wellington Reef) at Darwin Island remains in a positive growth mode. The remainder either degraded to a coral community or was lost. Retrospective analyses of the age structure of corals killed in 1983, and isotopic signatures of the skeletal growth record of massive corals suggest the occurrence of robust coral populations during at least a 500-year period before 1983. The greatest potential threats to the recovery and persistence of coral reefs include: ocean warming and acidification, bioerosion, coral diseases, human population growth (increasing numbers of residents and tourists), overfishing, invasive species, pollution, and habitat destruction. Such a diverse spectrum of disturbances, acting alone or in combination, are expected to continue to cause local and archipelago-wide mortality and degradation of the coral reef ecosystem.

1. Introduction

The following descriptions and definitions clarify terminology used in this review. The term “corals” refers to reef-building scleractinian corals that harbor endosymbiotic dinoflagellates (zooxanthellae). From

a global perspective, coral reefs in the Eastern Pacific are small, distributed discontinuously, less diverse, and less structurally robust compared to their counterparts in the Indo-West Pacific, Central Pacific and Caribbean (Cortés, 1997; Glynn, 2001). Furthermore, the 17 reefs that Glynn and Wellington (1983) documented, scattered across the

[☆] A Salute: This article acknowledges the pioneering work of Jerry (Gerard) M. Wellington who was the first to document systematically the occurrence and nature of coral communities and coral reefs in the Galápagos Islands, a biologically diverse and highly valued ecosystem in the Galápagos Marine Reserve.

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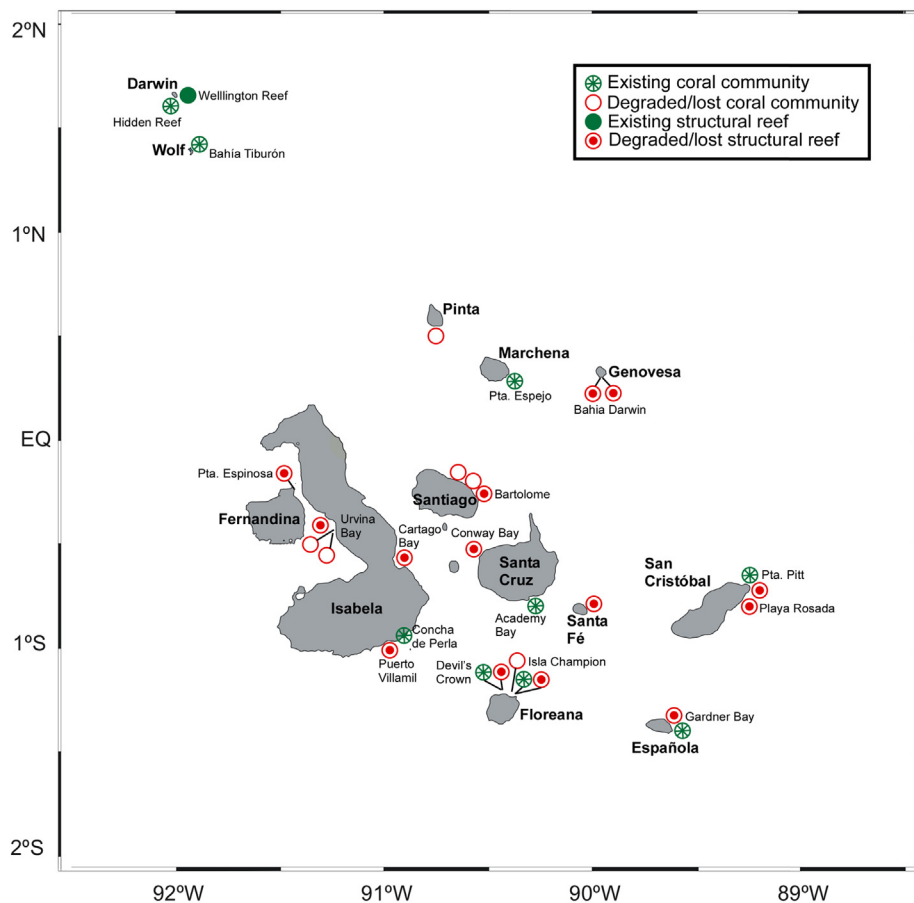


Fig. 1. Location and condition of coral reefs and coral communities in the Galápagos Islands, post 1982–83 El Niño event. Assessments were based on 42 years of surveys (1975–2017). In addition to the structural reefs indicated in this figure, two small pocilloporid patch reefs (now lost) were observed in Cormorant Bay (near Devil's Crown) and South Champion Island, for a total of 17 structural reefs existent prior to the 1982–83 ENSO.

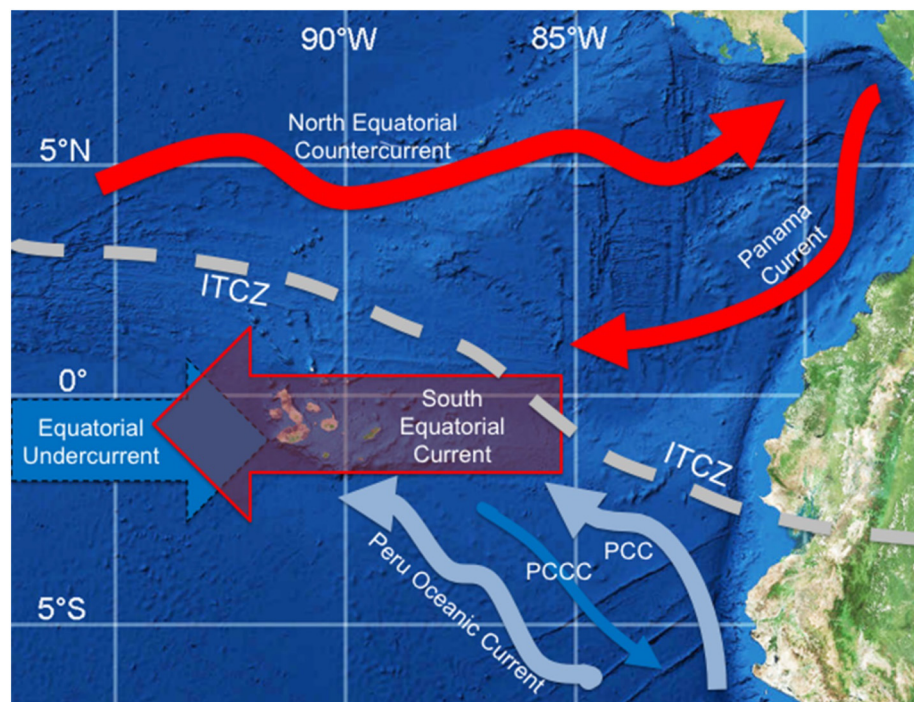


Fig. 2. Major oceanographic currents in vicinity of the Galápagos Islands. Warmer currents (red) prevail north of the Intertropical Convergence Zone (ITCZ) and cool currents (blue) south of the ITCZ. The ITCZ migrates 8–10° in latitude seasonally, from about 12° N in August to about 4° N in February (Cromwell and Bennett, 1959). The Equatorial Undercurrent and Peru Coastal Countercurrent (PCCC) are cool subsurface currents. PCC = Peru Coastal Current.

Archipelago, were even smaller in size and extent than those found elsewhere in the eastern Pacific. Glynn (2001) succinctly summarized the distinction between Eastern Pacific coral communities and structural coral reefs. “Coral reefs are wave-resistant limestone structures built dominantly by the vertical accumulation of coral skeletons. In

contrast, coral communities are loosely spaced to dense aggregations of coral colonies that veneer underlying substrates whose origin is other than the actively growing corals they support.”

Reef-building coral communities and coral reefs in the Galápagos Islands have experienced profound and overwhelmingly negative

changes since the early 1980s, during and following the unprecedented 1982–83 El Niño warming event. Located astride the equator in the eastern Pacific region (Fig. 1), from about 2.0° north to 1.5° south, the Galápagos Islands are subject to diverse and sometimes stressful marine and atmospheric conditions that undergo marked hourly, daily, seasonal and inter-annual variation (Houvenaghel, 1984; Chavez and Brusca, 1991; Banks, 2002). Such conditions often were cited in the early literature to explain the marginal nature of eastern Pacific coral reef development (e.g., Darwin, 1842; Dana, 1843).

Beginning in the 1970s, with an exponential increase in tourism and the requisite supporting infrastructure, additional human-related stresses (e.g., habitat destruction, over-fishing and pollution) have occurred and are continuing to affect the islands' biota (Alava et al., 2014; Vinueza et al., 2014). Thus, although their exact extents are unknown, both natural and anthropogenic stresses are presently affecting coral populations of the Galápagos Islands.

Here we examine the probable development of coral reefs in the Archipelago during the past seven centuries, its present state (including contemporary reef development and distribution), and offer projections of possible future changes. A range of physical and biological topics relevant to coral ecology is included in this review.

2. Oceanographic conditions relative to corals

2.1. The Galápagos Islands within a wider Pacific Ocean circulation context

The oceanographic setting of the Galápagos Islands (Fig. 2) underscores, shapes and characterizes local coral ecology through small and meso-scale ocean processes that are moderated and driven by wider ocean signals. Eastern Tropical Pacific (ETP) and Pacific basin circulation under seasonal, El Niño-Southern Oscillation (ENSO) modes and Pacific Decadal Oscillation (PDO) is evident through multi-decade ensemble satellite data (Feldman et al., 1984; Palacios, 2004; Schaeffer et al., 2008), ocean observations (Wyrтки, 1966, 1985a, 1985b; Houvenaghel, 1978; Enfield, 1989; Kessler, 2006; Sweet et al., 2009; McPhaden et al., 2011) and modeled data (Cravatte et al., 2007; Karnauskas et al., 2014; Liu et al., 2014). While eastern interconnections among the long zonal currents of the Eastern Pacific are still uncertain (Kessler, 2006) and model predictions do not yet agree as to future scenarios, the time series data has served to provide some insight into regional climate trends. However, it is obvious that large basin-wide climate signals greatly influence key physical processes over small spatial scales, and that abiotic conditioning at such scales is highly relevant to local Galápagos Islands coral ecology and survivorship.

The dominant westward surface flow influencing the Islands, often referred to as the South Equatorial Current (SEC), represents an amalgam of surface waters fed from the northeasterly edge of the south tropical gyre, linked to the strengthened Peru Oceanic and Coastal Current systems (or Humboldt flow) and reinforced by southeast trade winds during the Island's cool season (June–Nov). Being driven by wind and Coriolis forcing towards the west, cooler advected water is supplemented by Ekman upwelling at the North Equatorial Current and SEC divergence along the equator (typically referred to as the Equatorial cold tongue), extending from the coast of South America. During the warm season (Dec–May) as trade winds relax, there is increased advection of warmer, less saline waters extending from the north-east implicated with the deviation of the North Equatorial Counter Current as it approaches the Panama Bight (Fig. 2). This warmer influence provides a more stable warmer ocean regime throughout the year across the northerly coral communities of Darwin and Wolf compared to cooler conditions in the southern Archipelago.

Cool Equatorial Undercurrent (EUC) filaments, shoaling around the Galápagos platform and pinnacles as a compensatory sub-current from the west underlying surface flow, importantly influences cooler saline mixing, nutrient loading and flushing over subtidal reefs. Hence it is not uncommon to have particularly strong thermoclines under equatorial

heating, periodically disrupted by physical mixing of EUC water through bathymetric deflection. Wind driven upwelling, given the island positioning in flow paths and distinctive volcano topography, also generates uncommon scenarios where even northerly corals (at Darwin and Wolf Islands) are periodically subject to anomalous cold flushing and mixing of lower pH waters on the equator.

2.2. Climate trends

The timing, intensity and direction of dominant seasonal flows are subject to ENSO modulation. ENSO and longer timeframe PDO climate oscillations alter key productive processes, connectivity and gene flow potential, water geochemistry, mixing and thermo-saline properties and shoaling of the thermocline to the Eastern Pacific. Not surprisingly, this has had direct significance for the viability of key sessile habitat formers such as corals (most notably during the recent strong ENSO warm periods). As an observed example, Kelvin internal waves generated by wind anomalies that propagate eastwards from the western Pacific (as part of the underlying ENSO mechanism) can cause rapid anomalous temperature shifts through the periodic shoaling and deepening of the thermocline. Tropical instability waves are also consistent meso-scale features that generate undulating sea surface temperature and productive oceanic fronts across the northern pinnacles as they propagate towards the west at 2–4° N (Sweet et al., 2009). The resulting cooler flushing from depth over several weeks across northerly Galápagos coral communities into solar heated surface waters can generate 6–12 °C differences in temperature over short 4–6 day timescales. During such events *Porites lobata* were observed to cold-shock bleach alongside apparently healthy *Pavona* sp. colonies (Banks et al., 2009) and recover as conditions normalized.

The long-term warming trend of concern for increased bleaching, as evidenced in the western and central equatorial Pacific prior to 2000 (~2 °C decade⁻¹), is as yet not substantiated across the Archipelago. Despite ongoing increases in radiative forcing under a shifting global climate, it is still unclear how cool eastern Pacific sea surface temperatures have persisted in the past decade. At local scales Karnauskas et al. (2014) showed a slight cooling trend in western Isabela and suggested a possible insulating upwelling effect for the Galápagos region. Increased anomalous trade winds and resulting equatorial and boundary system upwelling are proposed as mechanisms essentially buffering surface temperatures across the Islands. Again it is unclear how long the warming hiatus will continue into the near future, although if winds abate, rapid warming under global forcing would potentially resume with significant local effects on seasonal maxima and associated systems (England et al., 2014).

Despite the recent SST observations, local temperature records based in Puerto Ayora, Santa Cruz Island since the 1960s do indicate a series of increasing temperature anomalies with cumulative degree heating and cooling events and associated temperature stress (Fig. 3a and b). Hence, while a global neutral SST trend is evident over the last 40 years (Wolff, 2010) there is also evidence of a net increase in cold and warm seasonality and distinct SST spatial patterning. Extinction risk for reduced populations such as corals in particular is considered to be much higher under such abrupt and more frequent disturbances when compared to a more gradual decadal shift.

3. Past climate from coral cores

Cores from individual coral colonies can provide a detailed description of the reef environment through time. In the main portion of the Galápagos Archipelago, however, most of the long-lived corals identified by Glynn and Wellington (1983) succumbed during the El Niño event of 1982–83, and their skeletons lost to bioerosion (Glynn, 1994). Fortunately for this type of retrospective analysis, in 1954, magma rose beneath Urvina Bay of western Isabela Island (Fig. 1) and lifted the coral communities above sea level, preserving this pre-1982-

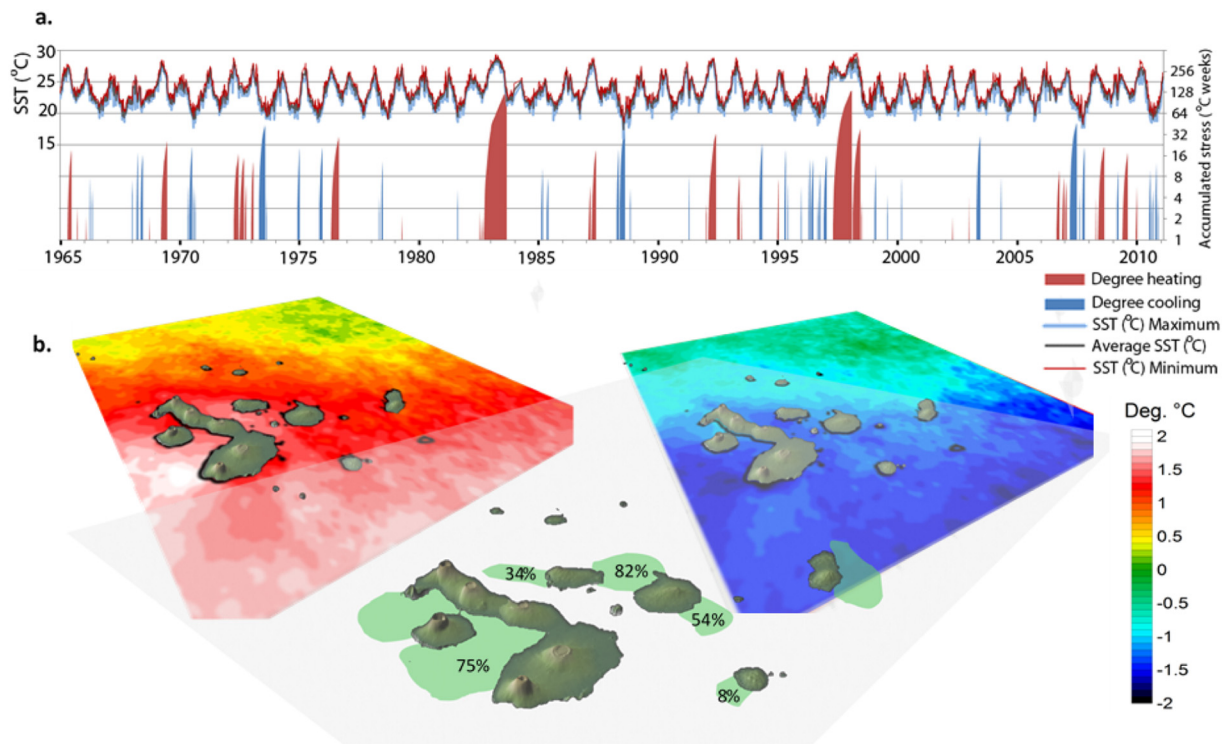


Fig. 3. (a) Galapagos heating and cooling stress events calculated from the 1965–2011 sea surface temperature record in Academy Bay, Santa Cruz. Stress indices are derived from sustained and accumulated degree heating and cooling weeks taken as the integration over time of temperatures that exceeded the global averaged minimum (cold) or maximum (hot) for each weekly period by more than 1 °C. (b) Sea surface temperature anomalies calculated from MODIS data for warm season (Dec–May left), cool season (Jun–Nov right) and % observed expression of Equatorial Undercurrent upwelled water following oceanographic cruise data 2004–2007 and MODIS-Aqua satellite derived chlorophyll and temperature fields (below, adapted from Schaeffer et al., 2008).

83 ENSO community (Couffer, 1956; Colgan, 1991). On the uplift, 17 isolated coral communities were found, and a core taken from the largest colony (*Pavona clavus*) that lived from 1583 to 1954 (Colgan, 1991; Dunbar et al., 1994). This 371-year old coral provided a record of past changes in growth rate and, via oxygen isotope analysis, ocean temperatures (Dunbar et al., 1994). Other coral core studies in the Galápagos Islands used much shorter cores, and/or focused on paleoclimate proxy development (see Cole and Tudhope, 2017, for a summary).

In the northern islands (Darwin and Wolf, Fig. 1), long-lived massive colonies have persisted to this day. Several of those that survived the 1982–83 event at Darwin and Wolf Islands have been cored for paleoclimatic and growth rate analysis, and a subset of these cores extends from present to well before 1982. Visual inspection of these cores clearly shows that they all experienced a growth hiatus (death horizon) during 1983, and that regrowth commenced within a few years. In contrast, all of these colonies grew without interruption through the strong El Niño event of 1997–98, which was nearly as extreme in terms of warming (Fig. 3a).

Systematic changes in the rate of growth remain difficult to determine. In principle, annual density bands can provide annual growth rates, but in practice the banding in these samples is not sufficiently resolved to rely on this method. Annual cycles in high-resolution geochemistry also reveal rates of growth, but this method demands intensive analytical effort. At Wolf Island, a 70-year record of coral strontium-calcium ratios (Sr/Ca) (Jimenez et al., 2018) shows annual rates of growth averaging $14 \pm 4 \text{ mm yr}^{-1}$. The high variability from year to year precludes identifying significant changes in growth rate, but ongoing analysis of additional cores may allow such patterns to be identified.

The Wolf Island record of skeletal Sr/Ca reflects past changes in local seawater temperature since 1940 (Jimenez et al., 2018). These data show strong variability associated with the seasonal cycle and with

El Niño extremes, including a $\sim 5^\circ\text{C}$ multi-month warming during the exceptional 1997–98 El Niño event, with no apparent interruption in growth. The northern islands are generally warmer than the main portion of the archipelago, where upwelling exerts a cooling influence (Fig. 3b). Analysis of instrumental temperature records in the southern and central islands has indicated little to no warming trend in recent decades (Wolff, 2010), leading to the suggestion that this area is insulated from the global increase in temperature (Karnauskas et al., 2014). However, Jimenez et al. (2018) suggest a small but identifiable warming at Wolf Island since 1940. This result suggests that the northern reefs, although they have been resilient to past warming stresses (Table 1), may find themselves vulnerable to the inexorable anthropogenic warming of ocean temperatures.

Other aspects of these cores deserve mention. First, significant bioerosion from lithophagous bivalves was observed in nearly every core. Second, the cores themselves, and the slabs derived from them, are fragile compared to similar samples from the same species elsewhere in the Pacific. Both of these features are consistent with skeletal weakness due to naturally low pH and carbonate levels in the Galápagos Islands (see “Climate change and ocean acidification” below, Manzello et al., 2008; Manzello, 2010). As atmospheric CO₂ rises and ocean pH declines, the ability to produce carbonate skeleton will become even more challenging for the corals that remain throughout the Galápagos Islands.

4. Pre-ENSO 1982–83

Assessments of the nature and condition of Galápagos corals and coral reefs preceding the 1982–83 El Niño disturbance are available in Durham and Barnard (1952), Durham (1966), Wellington (1975, 1984), Glynn et al. (1979), Glynn and Wellington (1983) and Glynn (1994, 2003). The elevated and prolonged seawater-warming event of the 1982–83 El Niño resulted in Archipelago-wide devastation of marine

Table 1
Modern coral age estimates based on sclerochronology and reef framework thickness measurements at various sites in the Galápagos Islands.

Measurement type	Species	Locality ^a	Growth axis (cm) ^b	Growth rate (cm/yr) ^c	Age (years) ^d	Comments, references	
Colony skeletal growth	<i>Porites lobata</i>	Floreana	218	0.81	262	All colonies mostly dead or severely eroded when sampled in 1989. Glynn and Wellington, 1983; Glynn, 1990, 1994; Colgan, 1990	
		San Cristóbal	215	0.81	258		
		Santa Fe	289	0.81	347		
		Santa Cruz	146	0.81	175		
		Isabela	150	0.81	185		
		Santiago	315	0.90 ^e	350		
	<i>Pavona clavus</i>	Floreana	529	1.2	441	<i>Pavona clavus</i> data for Isabela Dunbar et al., 1994	
		Santa Cruz	122	0.80	98		
		Isabela ^f	500	1.4	366		
			100	1.4	71		
	Reef framework accretion ^h	<i>Pavona gigantea</i>	Genovesa	300	1.2	250	Topped, dead colony, radiocarbon dated. Macintyre et al., 1992 Radiocarbon dating of samples collected in 2012 from bases of framework towers Glynn et al., 2015
			Champion	215	2.0	420	
		<i>Porites lobata</i>	Darwin ^g	120	0.19	625	
				180	0.34	535	
			250	0.36	690		
			230	0.34	665		
			170	0.29	590		
<i>Pocillopora elegans</i>			90	0.15	595		
		Floreana	270	0.56	480	Vertical framework heights of live reefs measured in 1975 and 1976	
		Devil's Crown	60	0.56	110		
	Champion	100	0.56	180			
San Cristóbal	100	0.53	189				
	Genovesa	100	0.53	189			

^a Site locations are available in the references listed.

^b Maximum colony sizes and continuous reef framework accumulations were measured in situ.

^c Maximum colony skeletal growth measured from x-radiographs in cut sections of corals and from vertical heights of uninterrupted reef frameworks.

^d Live coral age estimates from times sampled, noted in “Comments and References” column.

^e Marchena colony growth rate applied.

^f The two colonies of *P. clavus* sampled at Isabela Island from the Urvina Bay shelf, uplifted in 1954 (Couffer, 1956; Malmquist et al., 1986).

^g Sampling site was the Wellington Reef.

^h Corals noted were the predominant species constituting the frameworks.

life (Robinson and del Piño, 1985). Coral bleaching and mortality were severe throughout the islands, with overall 97% mortality at 14 surveyed sites (Glynn et al., 1988). This high and widespread degree of coral mortality, observed generally in the equatorial eastern Pacific following the 1982–83 El Niño event, was at the time unprecedented in the scientific literature.

Archipelago-wide surveys conducted in the 1970s identified 17 structural coral reefs on 10 islands and numerous coral communities on 14 islands (Fig. 1), all in a healthy state (Wellington, 1975; Glynn and Wellington, 1983). Sclerochronological evidence, i.e. the sizes and ages of massive coral species and the development of coral reef framework structures at that time, suggest that Galápagos corals thrived for several hundreds of years before the devastating El Niño warming event of 1982–83. Despite sporadic, short-term skeletal hiatuses, peripheral coral growth appears continuous. Such periods of uninterrupted coral colony growth and reef framework accumulation have been identified at several island sites to gain insight into the existence of coral growth in the recent past, namely prior to 1982–83. These estimates were calculated from pre-1982–83 measurements conducted across the Archipelago (Fig. 1, Table 1). Assuming continuous growth of massive corals and accumulation of reef frameworks, the quantification of such processes should provide a measure of favorable periods of coral development. By these estimates, the majority of sampled massive coral colonies (*Porites lobata*, *Pavona clavus*) exhibited continuous growth for 100–300 years. A few colonies (*Pavona clavus*) exhibited uninterrupted growth for 250 to a maximum of 441 years off the northeast coast of Floreana Island. Reef framework accretion rates are typically lower than colony skeletal growth due to bioerosion, sediment compaction, structural collapse and material transport. Pocilloporid framework block thicknesses indicated continuous accretion during 107–122 years at most sites, and several reefs exhibited 179–204 years of uninterrupted growth. One fringing pocilloporid reef on the northeastern

coast of Floreana Island revealed a vertical reef-frame thickness of 2.7 m, equivalent to 480 years of accretion.

Structural coral reef age estimates reported for the Wellington Reef at Darwin Island revealed ages ranging from 500 to nearly 700 years (Glynn et al., 2015). Radiocarbon dating of *Porites lobata* samples from the bases of coral framework stacks ranged from 535 to 690 yr BP. These 0.9–2.5 m-high stacks, indicative of rapid carbonate accretion, are equivalent to framework growth rates of 1.5–3.5 m Kyr⁻¹, which are comparable to the fastest known coral reef growth rates in the Indian and Central/Western Pacific Oceans (Montaggioni, 2005).

5. Post ENSO 1982–83 to 2017

Of the 17 known structural coral reefs present in the Archipelago in 1976 (Fig. 1), all but one, the Wellington Reef¹ at Darwin Island, have disappeared (bioeroded to sediments) or been severely degraded after 1983. Remnants of large pocilloporid reefs were discovered later at Puerto Villamil (Isabela Island) and at Playa Rosada (San Cristóbal Island), but the cause(s) and time of their demise are unknown.

A second very strong ENSO event occurred in 1997–98, however there was much less direct and subsequent impact to corals compared to the 1982–83 event (Glynn et al., 2017a, 2017b). This is likely due to coral survivors of the 1982–83 event possessing a genetic predisposition (in themselves and their zooxanthellae) for resistance to warm conditions (see Section 6 below).

The coral reef at Devil's Crown (Floreana Island) demonstrated notable recovery from 2000 to 07, but then experienced high mortality (95%) coincident with a La Niña cooling event (Feingold and Glynn, 2014) followed by another recovery through 2017 (see Section 13 below; Baker et al., 2008). Cold water shock was also observed in the

¹ The reef name honors the late Jerry (Gerard) M. Wellington.

northern Islands in 2007, which caused coral bleaching and some tissue mortality (Banks et al., 2009; Glynn et al., 2017a, 2017b). This event, a result of internal waves forcing cool water upwards above the thermocline, amounted to a 12 °C drop in temperature over a 6-day period. A notably high incidence of coral health anomalies (trematodiasis, tissue discoloration, uncharacterized diseases, etc.) in the northern Islands prompted Vera and Banks (2009) to suggest this could be a result of a tendency towards more frequent warm-water and cold-shock bleaching events.

6. *Symbiodinium* diversity and community dynamics

Symbiodinium is the photosynthetic dinoflagellate endosymbiont found within coral tissues. *Symbiodinium* produces excess photosynthate, a very important source of energy for reef-building coral colonies, often comprising over 90% of the coral's energy budget. Since the taxonomy of *Symbiodinium* is not clear, the term “clade” is used to denote populations with distinct physiological properties (e.g. differing photosynthetic efficiency at different temperatures).

The first surveys of *Symbiodinium* in Galápagos corals were undertaken in the central and southern islands (Santa Fé, Marchena and Santa Cruz) during the 1997–98 El Niño event (Baker, 1999). Samples collected prior to bleaching in June 1997 were found to contain a variety of *Symbiodinium* in clade C, but no members of clade D. Samples collected during the bleaching event in March 1998 also found clade D to be rare, although they were found in some healthy colonies of *Pocillopora* that were unaffected by bleaching, and were also detected as the residual symbionts in two moribund *Pocillopora* colonies (Vandepas et al., 2008).

A subsequent survey of *Pocillopora* in the Galápagos Islands found this coral host associated with *Symbiodinium* C1b-c, C1d, and D1 (Pinzón and Lajeunesse, 2011; Cunning et al., 2013; Baums et al., 2014). The taxonomic status of *Pocillopora* spp. is under dispute, with several morphotypes being described either as separate species or types, depending on the authority. In the Galápagos, only *Pocillopora* type 1 and type 3 have been recorded to date (Pinzón and Lajeunesse, 2011; Cunning et al., 2013; Baums et al., 2014) and both of these *Pocillopora* types appear capable of hosting *Symbiodinium* D1, although type 1 appears to do so more commonly than type 3 (Cunning et al., 2013). A large aggregation of *Pocillopora* at Isabela Island (the result of asexual reproduction of a single founder colony that is the only representative of type 3a in the Galápagos) was found to be dominated by *Symbiodinium* C1d (Baums et al., 2014).

Symbiodinium D1 (also referred to as *S. glynnii*, Wham et al., 2017) is a thermotolerant symbiont preferentially retained by hosts during bleaching episodes (Glynn et al., 2001; Cunning et al., 2013), resulting in community changes in favor of these symbionts during recovery (Baker et al., 2004). Microsatellite surveys of *Symbiodinium* D1 found they were part of a population of *Symbiodinium* D1 that is well connected throughout the Galápagos Islands, Clipperton Atoll, Panamá and southern Mexico, but distinct from the D1 population in the Gulf of California (Pettay and Lajeunesse, 2013). However, to date *Symbiodinium* D1 has been found only in pocilloporid hosts in the Galápagos, suggesting that these thermotolerant symbionts may be limited in their partnerships with other scleractinian species.

Porites lobata collected from Darwin and Wolf Islands in March 2006 were all found to contain *Symbiodinium* C15, or variants thereof (Glynn et al., 2009), and related *Symbiodinium* C1-types were found in the scleractinian genera *Pavona*, *Diaseris* and *Psammocora* in 1997–98 (Vandepas et al., 2008). Surveys of zooanthid corals from similar environments in the Galápagos found that zooanthellate *Palythoa* and *Zoanthus* contained only *Symbiodinium* C-types that, as C1/C3 variants, were likely similar to the C1-types found in scleractinian hosts (Reimer and Hickman, 2009).

Symbiodinium D1 is relatively rare in the Galápagos Islands, despite being comparatively common at other sites in the far eastern Pacific,

such as Panamá and Mexico (Baker, 1999; Glynn et al., 2001; Baker et al., 2004; Iglesias-Prieto et al., 2004; LaJeunesse et al., 2008; Pettay et al., 2011; Pettay and Lajeunesse, 2013; Walther-Mendoza et al., 2016; Baker et al., 2017). It appears to be more common in *Pocillopora* in the northern Galápagos (A. Palacio, unpubl. data), but its comparative scarcity overall may explain why bleaching-related mortality was relatively higher in the Archipelago during both the 1982–83 and 1997–98 El Niño events, compared to elsewhere in the Eastern Pacific.

It has been suggested that the normally cool waters of the Galápagos tend not to favor dominance by thermotolerant *Symbiodinium* D1, resulting in these coral communities being particularly susceptible to the effects of high temperature bleaching (Vandepas et al., 2008). The 2014–16 El Niño event will provide an opportunity to test the hypothesis that episodic thermal stress can increase the abundance of *Symbiodinium* D1 in *Pocillopora*, and potentially also inject D1 into other non-pocilloporid hosts. Such changes, if they occur, will likely boost the future thermal tolerance of these coral hosts, but may also result in slower growth or other physiological tradeoffs, although the strength of these tradeoffs is likely to be environment-dependent (Cunning et al., 2015).

7. Coral resilience and recovery

The size structure of coral populations is responsive to disturbance history and specific types of impact can be detected by specific patterns of size-shifts (Bak and Meesters, 1998; Bauman et al., 2013; Riegl and Purkis, 2015; Riegl et al., 2017). Severe mortality will obviously remove most corals and will lead to dominance by small corals during the regeneration phase. Since these will grow out to become larger, populations further down the path of re-establishment will have an increasing share of larger size-classes (bearing in mind that not all corals reach equal size, thus size-classes need to be standardized for each species; Riegl et al., 2017). This process should provide a convenient means of identifying progress in regeneration, which can serve as proxy for the time to a past disturbance, its severity, or the rate of regeneration.

Corals in the Galápagos Islands exist under widely varying environmental conditions, since strong gradients exist due to the region's varied oceanographic regimes (Fig. 2; Fiedler and Lavin, 2017). Only the northernmost islands (Darwin and Wolf) fall into a regime that is typically considered to be within the sedimentological “reef window”, where long-term conditions can clearly be considered suitable for tropical corals and the resultant framework accumulation (Humphreys et al., 2016; Raymond et al., 2016). While previously some modest framework build-ups have existed in many islands of the southern Archipelago, presently only a single island has a fully-developed reef (Wellington Reef on Darwin; Glynn et al., 2015, 2017a, 2017b). Repeated impacts since the 1982–83 ENSO event (Glynn, 1988b, 1990) have disadvantaged corals, and frameworks and skeletons were degraded by intense bioerosion (Glynn et al., 1979; Glynn, 1994, 1997; Reaka-Kudla et al., 1996). However, locally robust regeneration has also been observed (e.g. see Section 13 below).

Size-structure in Galápagos Islands' corals clearly expresses the history of past disturbances and stresses. It differentiates along vertical (depth) and horizontal (latitude, exposure) gradients. At Wolf Island, the only island where uninterrupted coral growth occurs from sea level to the lower depth limit, coral sizes show a maximum at around 15 m depth with minima in the shallowest and deepest depths (Fig. 4; Glynn et al., 2015). This is attributed to wave action on unstable substrata (e.g. boulders) disadvantaging shallow corals, and the obvious light limitations in the deeper areas.

The size-class distributions of the long-lived coral *Porites lobata* (Fig. 5), among the most important reef-builders in the tropical eastern Pacific, showed the greatest population resilience at the central and northern islands of Marchena, Darwin and Wolf. The greatest frequency of large, old corals in the Archipelago occurs at Darwin and Wolf

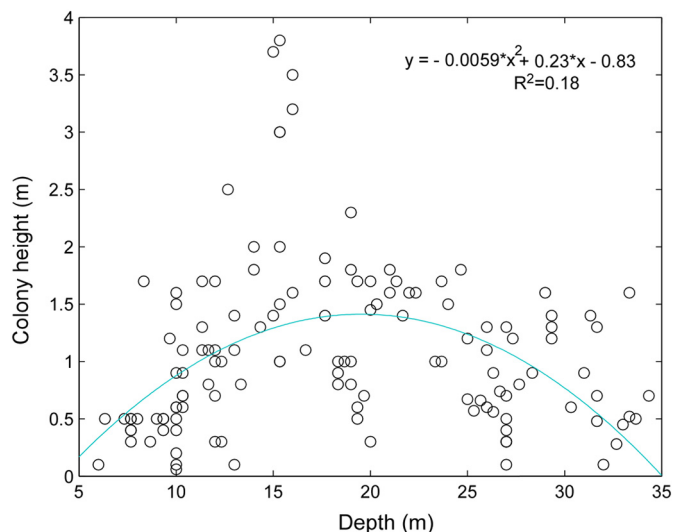


Fig. 4. Size distribution (vertical extent of colonies) of *Porites lobata* at Wolf Island, northern Galápagos Islands. Modified after Glynn et al., 2015.

Islands. These colonies survived the stresses of the 1980s and 1990s (skeletal growth radii > 30 cm), suggesting greatest population resilience there. Corals at Darwin, impacted severely during the 1982–83 event (Glynn, 1990, 1994; Glynn et al., 2015), displayed a peak in the 30 cm size-class suggesting a recruitment pulse just after the mass mortality event. The size-distribution at Marchena Island suggested good recruitment and regeneration from a severe disturbance that had degraded virtually all large colonies about 30 years ago (likely the 1982–83 event). In the southern islands (with the exception of Devil's Crown, Floreana Island), *P. lobata* is rare and occurs primarily as small colonies, most of which are younger than 30 years, and therefore represent regenerative growth after the 1982–83 ENSO.

8. Deep coral communities

Coral communities deeper than 20 m have received comparatively little attention in the Galápagos Islands. However, general interest in deeper coral communities as refugia from disturbance has surged in recent years (Bongaerts and Smith, in press) and one refugium has already been posited for a hydrocoral in the eastern Pacific (Smith et al., 2014). Thus, an examination of deeper coral communities in the Galápagos, with its history of extreme thermal disturbance, is warranted. Areas with extant or historical presence of shallow water corals and coral reefs were surveyed for deeper corals at depths to 30 m across the Archipelago in 2012.

Areas where deeper coral communities were found were more systematically sampled from 2014 to 2017. As is typical in the eastern tropical Pacific (Smith et al., 2017), it appears that upwelling and shallow thermocline depths (< 20 m) limit deep coral development throughout much of the southern and western archipelago (Fig. 6). As noted in Section 13 below, a deeper free-living fungiid coral community at 13–34 m depth was described off the northern coast of Floreana Island (see also Wellington, 1975; Feingold, 2001; Feingold and Glynn, 2014). This same location supports massive coral (*Pavona gigantea* and *Pavona clavus*) development to depths of about 25 m. In the northern Galápagos Islands, well-developed coral communities occur at Bahía Tiburón, Wolf Island to 30 m depth, with scattered corals to 40 m (Fig. 6). At Wellington Reef, Darwin Island, corals are abundant to about 22 m, but are fewer in number at greater depths due to an unstable sediment apron that begins at 22–30 m depth. Coral species present at this site include *Pavona clavus*, *Pavona gigantea*, *Pavona varians*, *Gardineroseris planulata* and *Porites lobata*. Species such as *P. lobata* occur abundantly to depths > 50 m at Clipperton Atoll in the eastern

Pacific (Glynn et al., 1996). This suggests that massive species such as *P. lobata* can occur deeper than 40 m and that the lower limit (22 m) of coral at Wolf Island is a local limit due primarily to sub-optimal thermal conditions. Darwin Island benthic temperatures at 30 m showed regular excursions below 20 °C and a minimum temperature of 14.4 °C (period of measurement: June 2012–February 2016), whereas at 20 m excursions below 20 °C were rare (period of measurement: July 2015–March 2017). While more areas need to be surveyed below depths of 20 m, it appears that there are potential depth refuge populations between 20 and 40 m depth in the Galápagos, particularly in the northern-most islands.

9. Coral genetic revelations

9.1. *Pocillopora* sp.

Genetic and genotypic diversity of coral populations is a key driver of recovery from severe disturbances (Baums, 2008). Genotypic diversity, or the number of distinct genets in a population, is closely tied to successful sexual reproduction in many reef-building species. Self-incompatibility in hermaphroditic species, combined with variable inter-genet fertilization rates (ranging from 10%– > 90%), contributes to this genotypic diversity (Willis et al., 1997; Baums et al., 2013; Miller et al., 2017). The discovery of a dense stand of 1614 live *Pocillopora* sp. colonies on Isabela Island (Concha de Perla lagoon, Fig. 1) in 2012 was thus exciting as it could have indicated a source population for sexual recruits to nearby habitats (Baums et al., 2014). However, multi-locus genotyping showed that this was unlikely. The Isabela *Pocillopora* colonies consisted of just one host genotype that reproduced via fragmentation. These corals were identified as belonging to the host mitochondrial open reading frame lineage type 3a not found elsewhere in the Galápagos Islands (and all harbored *Symbiodinium* ITS-2clade C1d). Demographic modeling suggested that the first colony of this genotype settled here after the 1982–83 ENSO event but prior to the 1997–98 ENSO event. This suggests a locally successful but rare pioneer with little potential to contribute to the future of this lineage in the Galápagos Islands, until the time that a mate arrives. Continuous monitoring of coral habitats might reveal previously undetected colonies or new arrivals – either finding would lead to a welcomed re-assessment of the evolutionary potential of this species in the Galápagos Archipelago.

9.2. *Porites* spp.

Porites lobata is a predominant reef-building coral in the Galápagos Islands and the eastern Pacific region. Genetic studies by Forsman et al. (2009) classified several colonies of field identified *P. lobata* as closer to *P. evermanni*. Subsequent work by the Baums' laboratory confirmed this finding showed that, while difficult to distinguish visually, *P. lobata* and *P. evermanni* occur throughout the eastern Pacific region, including the Galápagos Islands. Yet the two *Porites* species differ in their bleaching response despite harboring the same species of *Symbiodinium*, providing rare evidence for the importance of the host in driving bleaching patterns (Boulay et al., 2014). Asexual reproduction via fragmentation occurs in both species but at differing rates across the region. This is partly explained by an intriguing three-way interaction between symbiotic bivalve mollusks (*Lithophaga* spp.) and the two *Porites* species. *Lithophaga* bore into the *Porites* skeleton and weaken it so that triggerfish (*Pseudobalistes naufragium*) preying on the bivalves generate coral fragments. This occurs more frequently in *P. evermanni* due to its higher infestation rate of bivalves compared to *P. lobata*. This leads to increased importance of asexual fragmentation as a means of population maintenance in *P. evermanni* along the Central American coastline. The dynamics differ across the region however, because *P. naufragium* occurs only sporadically in the Galápagos Islands as a transient during ENSO events. Instead, genotypic diversity of *Porites* populations in the Galápagos Islands might be driven by the interaction between skeletal

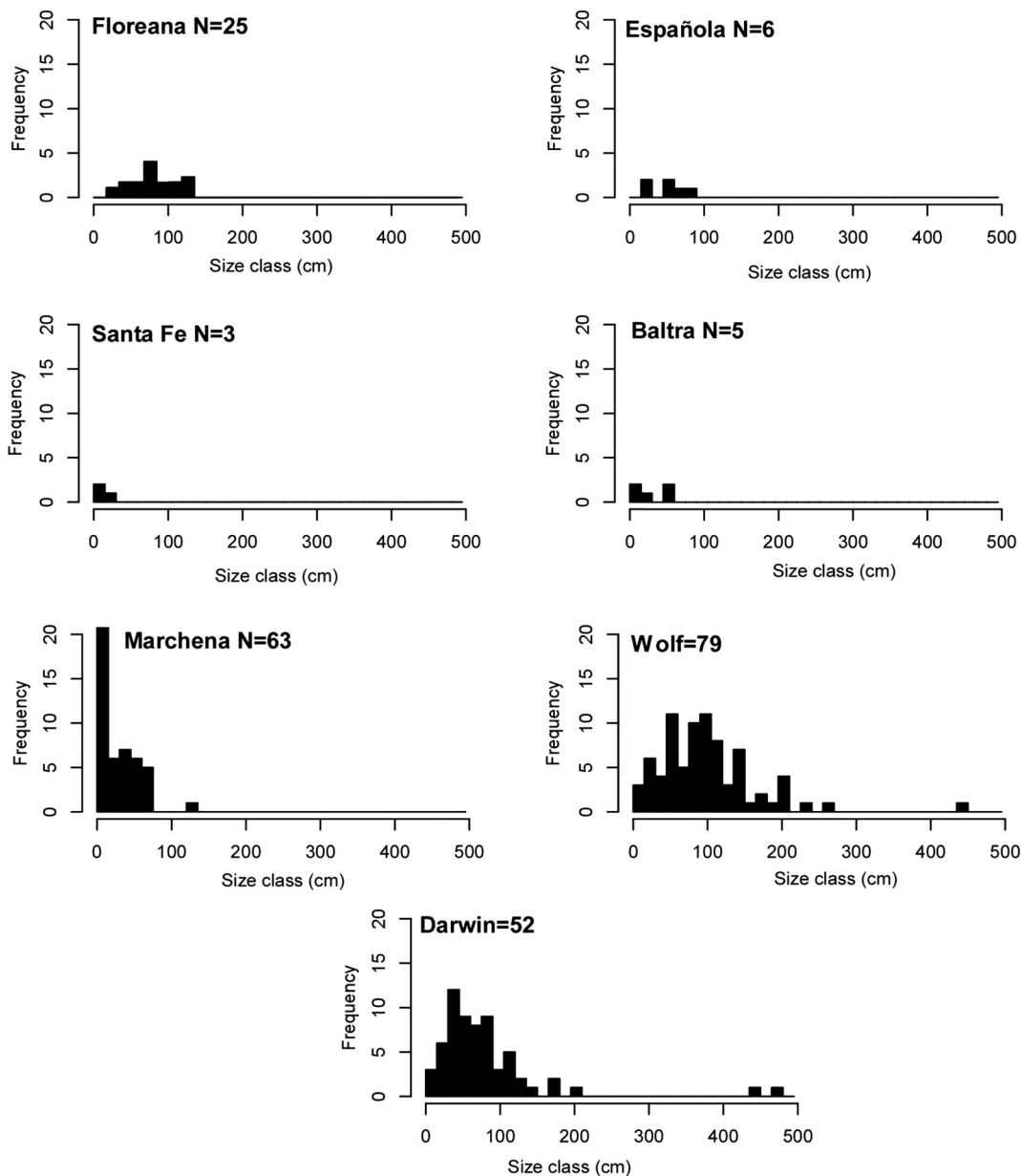


Fig. 5. Size-classes (defined by maximum diameter) of *Porites lobata* colonies across the Galápagos Islands. Data collected during June 2011, 2012 and 2013.

density and bioeroding sea urchin populations (*Eucidaris galapagensis*). Surveys of clonal reproduction via microsatellite genotyping of *Porites* spp. show that the southern island populations rely more heavily on asexual reproduction than populations in the north at Darwin and Wolf

Islands (Baums et al., unpubl.). *Porites* skeletons are less dense in the south and bioeroding sea urchin population densities are higher (Colgan, 1991; Manzello et al., 2014; Glynn et al., 2015). Both factors may contribute to higher rates of colony fragmentation in the southern

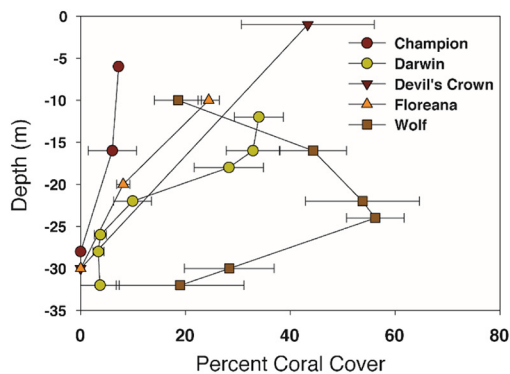


Fig. 6. Live coral cover (\pm SEM) at extant and historical Galápagos coral reef sites as a function of depth measured in replicate video transects in June 2012. Not shown is Urvina Bay, Isabela Island, with 0% coral cover across all sampled depths (1–32 m). Photograph is of a *Pavona clavus* colony (~80 cm high) and other corals present on basalt boulders at 30 m depth at Wolf Island (12 March 2017).

islands.

10. Coral-algal interactions

Early studies of the algae of the Galápagos Islands reported a diverse and abundant flora, despite the limitation that collections were largely restricted to species found intertidally (Farlow, 1902; Dawson, 1961, 1963). Dawson (1961) remarked that the flora of the Galápagos Archipelago showed such strong affinities with that of Mexico and Central America that he included the entire northeast Pacific in his checklist, from Ecuador and the Galápagos Islands to the Aleutian Islands. At present, the Charles Darwin Research Station database contains 482 algal records (CDF, 2018, FCD-DPNG marine database). Overall, the high diversity of algae that exists in the Galápagos Islands is likely associated with the complex oceanography of the region, which includes unique currents and oceanographic features that support a variety of habitats within a relatively small area (see Section 2 above).

Key concerns for the algae of the Galápagos Islands include potential extinctions and invasions. Edgar et al. (2010) reported that, among other taxa, six species of brown algae and nine species of red algae are now recognized as globally threatened, while six others are possibly extinct (*Dictyota galapagensis*, *Spatoglossum schmittii*, *Desmarestia tropica*, *Phycodrina elegans*, *Gracilaria skottsbergii* and *Galaxaura barbata*). Further, Keith et al. (2016) noted that two algal species have recently become invasive, *Caulerpa*, putatively *racemosa*, and *Asparagopsis taxiformis*. It is also possible that another species of *Caulerpa*, putatively *chemnitzia*, found overgrowing corals and other benthic reef organisms, is invasive. However, fully understanding the invasive status of *Caulerpa* is difficult as species within this genus are currently being reorganized and renamed based on molecular genetic evidence (for examples see Belton et al., 2014; Draisma et al., 2014). Further, although *C. racemosa* has been reported as present in the Galápagos Islands from 1899 (Farlow, 1902; Taylor, 1945; Dawson, 1961, 1963; Sylva, 1966) to the present (Bustamante et al., 2000; Danulat and Edgar, 2002; Keith et al., 2016) it has been argued this species is invasive because it recently increased its distribution and responds to changes in water temperature by expanding and contracting its abundance. Observations of spatial and temporal changes in the distribution and abundance of *C. racemosa* and *C. chemnitzia* suggest that they may be competing with coral and other sessile organisms (Keith, pers. obs.). The competitive status of these algae and their impact on corals are important avenues for future research as members of this genus have a long history of being invasive and causing major ecosystem impacts (e.g., Fernández and Cortés, 2005; Klein and Verlaque, 2008; Pérez-Estrada et al., 2013).

11. Coral-fish interactions

Coral-fish interactions have been studied worldwide, and include direct and indirect positive, negative, mutualistic and commensal effects (e.g. Bell and Galzin, 1984; Munday, 2004; Hughes et al., 2007; Rotjan and Lewis, 2008; Burkepile et al., 2013). However, these interactions are most clearly documented in areas with extensive coral reef development. In the Galápagos Islands, abundant coral cover only exists in relatively few places, most notably the far northern islands of Darwin and Wolf, and at a few sites in the central and southern islands (Fig. 1); other locations generally support scattered epilithic corals in areas dominated by rocky reefs (Glynn and Wellington, 1983). In these areas, which include the vast majority of the shallow coastal environment in the Galápagos Islands, fishes are not likely to interact strongly with corals. Still, coral-fish interactions in the Archipelago are likely to fall into similar categories as other coral reef systems: corallivory, coral as habitat and indirect effects (Bellwood et al., 2004).

Fish corallivory has been widely studied throughout the eastern Pacific (reviewed by Enochs and Glynn, 2017), and is likely the clearest and strongest example of coral-fish interactions. There are at least 25 species of facultative corallivores found in Galápagos, the most studied

of which is *Arothron meleagris*. In other parts of the eastern Pacific, this species appears to be a nearly-obligate coral feeder, with coral comprising 75–90% or more of its diet (e.g., Glynn et al., 1972; Guzmán and Robertson, 1989; Guzmán and Lopez, 1991). This species can be locally abundant in coral-dominated areas, and even though it may remove over 15% of coral carbonate production, the net impacts on coral predation appear to be minimal (Palacios et al., 2014). Indeed, unconsumed fragments from *A. meleagris* predation may facilitate asexual propagation in some coral species (Enochs and Glynn, 2017). However, *A. meleagris* is not abundant in Galápagos, with average densities of 7.8 ind ha⁻¹ across the Archipelago and 27.4 ind ha⁻¹ in the far northern islands where coral community development is most extensive (Edgar et al., 2004). These values are generally lower than those reported throughout the rest of the eastern Pacific (Palacios et al., 2014), so the net impact of *A. meleagris* corallivory may be lower in the Galápagos than at other eastern Pacific locations.

Other species of fishes likely also feed on corals in the Galápagos Islands, most notably parrotfishes (family Scaridae) and damselfishes (family Pomacentridae), as well as species from at least five other families. The impacts of these species have been extensively documented in other areas (e.g. Rotjan and Lewis, 2008); parrotfishes are likely targeting coral for the coral tissue itself and/or for endolithic algae, while damselfishes are most likely removing coral tissue to create substrate for their algal gardens (e.g. Ceccarelli et al., 2001). However, none of these species appears to be coral obligate feeders in Galápagos. Of the corallivorous species listed in Enochs and Glynn (2017), only one (*Melichthys niger*) has a density of more than two-fold higher in the far northern islands—where coral cover is highest—than any other region of the Archipelago (Edgar et al., 2004). Individuals of *M. niger* are often found around rock walls and drop-offs common in the northernmost islands, however, and are likely not feeding primarily on corals (Grove and Lavenberg, 1997). While the impacts of corallivorous fishes in the Galápagos Islands are likely to be low, none of these potentially corallivorous species has been studied in Galápagos and there are no published survey data of bite scar density. As a result, we do not yet know what effects fish corallivory may have in this Archipelago.

In other coral reef areas, many fish species use corals as obligate habitat (e.g. Munday, 2004 and references therein). There are no reports of coral-obligate fishes in Galápagos, however, and many genera that are coral-associated in other locations appear to be able to use rocky reef habitat in Galápagos (Grove and Lavenberg, 1997). Indeed, coral-obligate fishes would have very limited ranges in Galápagos and would be likely to suffer local extinction during the extreme oceanographic events (ENSO) that periodically reduce coral abundance archipelago-wide (Glynn, 1994; Edgar et al., 2010).

Indirect impacts of fishes on corals are likely to be the most ecologically significant coral-fish interactions, but as in other systems, understanding these indirect effects is challenging. In the Galápagos Islands, the most important of these indirect effects are likely mediated through the sea urchin *Eucidaris galapagensis* (Glynn et al., 2017a, 2017b). This sea urchin can be locally abundant, with densities to 30–90 m⁻² (Glynn et al., 1979; Glynn and Wellington, 1983), and it can have significant negative impacts on corals, both through direct coral predation and through bioerosion (Glynn et al., 1979; Glynn and Wellington, 1983; Reaka-Kudla et al., 1996; Glynn et al., 2015; also see Section 14 below). Several fish species, some of which are subject to fishing pressure, prey on these sea urchins. Observational and experimental studies suggest that removal of sea urchin predators via fishing may have cascading negative impacts on corals (Ruttenberg, 2001; Edgar et al., 2010, 2011; Dee et al., 2012). Unfortunately, there is ample evidence that fisheries have significantly reduced the abundance of major predatory fish species (Ruttenberg, 2001; Edgar et al., 2010, 2011; Usseglio et al., 2016), and lack of effective enforcement of fishery regulations suggests that trophic release of sea urchins is likely to continue (Hearn, 2008; Jones, 2013; Zimmerhackel et al., 2015). Other indirect coral-fish interactions likely exist in the Galápagos Islands,

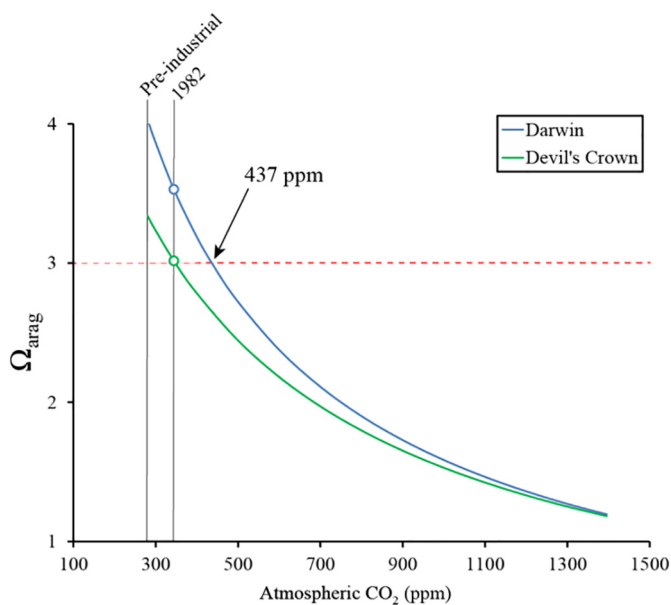


Fig. 7. Aragonite saturation state (Ω_{arag}) as a function of atmospheric CO_2 for Darwin and Devil's Crown, Floreana. Ω_{arag} values modeled as described in Manzello et al. (2013) by assuming a 1 ppm change in atmospheric CO_2 equals a $1 \mu\text{atm}$ change in seawater pCO_2 . Mean values of the seawater CO_2 system measured at Darwin and Devil's Crown in 2012 (Manzello et al., 2014) were used to model past and future Ω_{arag} values by assuming constant total alkalinity and salinity, and modifying seawater pCO_2 according to the relative change in atmospheric CO_2 . Ω_{arag} was calculated using the average annual temperatures for each location as reported in Manzello et al. (2014). Atmospheric CO_2 has increased approximately 52 ppm from June 1982 to June 2012 at the Mauna Loa observatory (NOAA ESRL, 2017).

such as indirect positive effects of herbivore grazing on algae (Hughes et al., 2007) and input of nutrients from fish sheltering near corals (Burkepile et al., 2013). However, these ecological pathways have not yet been examined. In addition to coral-algal and coral-fish interactions, coral-invertebrate effects are of paramount importance and are considered in Section 14 below.

12. Climate change and ocean acidification

Rapidly increasing atmospheric CO_2 is changing Earth's climate, causing ocean warming and acidification that are negatively impacting coral reefs (Hoegh-Guldberg et al., 2007). Reef-building corals exist within a limited range of temperatures and slight deviations ($1\text{--}2^\circ\text{C}$) above or below climatological highs and lows, respectively, cause coral bleaching and mortality (Hoegh-Guldberg et al., 2007; Lirman et al., 2011). The oceanic uptake of anthropogenic CO_2 is lowering seawater pH and the saturation state of aragonite (Ω_{arag}) (Caldeira and Wickett, 2003). This process, termed ocean acidification, is depressing coral calcification and stimulating biologically-mediated chemical dissolution (Albright et al., 2016; Enochs et al., 2016).

Surface waters in many parts of the eastern tropical Pacific (ETP) have lower pH and Ω_{arag} than the rest of the tropics because upwelling in this region brings CO_2 -enriched deep waters to the surface (Manzello et al., 2008). The Galápagos Islands are strongly influenced by upwelling due to the interaction of several major oceanic currents within the Archipelago (Schaeffer et al., 2008; see Section 2 above). The intensity of upwelling is greatest on the western shores of Isabela Island, and decreases from the southern to northern Galápagos Islands (Fig. 3b). Coral reefs in the southern Galápagos Islands experience low Ω_{arag} , currently encompassing what reefs globally will experience with a doubling and tripling of atmospheric CO_2 (Manzello et al., 2008; Manzello, 2010). In addition to experiencing naturally high CO_2

conditions, the Galápagos also experience periodic warming events associated with the El Niño–Southern Oscillation (ENSO), making the Archipelago an ideal natural laboratory for understanding the response of coral reefs to warming and acidification.

Since the 1982–83 ENSO warming event, the persistence of reefs around the Galápagos Islands has differed across an upwelling-induced acidification gradient. Reefs have all but disappeared in the southern Islands where $\text{pH} < 8.0$ and $\Omega_{\text{arag}} \leq 3$ with only modest recovery, whereas one reef (Wellington Reef) at the northern-most island of Darwin has persisted where $\text{pH} > 8.0$ and $\Omega_{\text{arag}} > 3$. The mechanisms driving the disparate trajectories are hypothesized to be due to regional differences in carbonate cementation, coral skeletal density, and bioerosion across the northern and southern islands. In the southern islands, calcium carbonate cementation, which acts to bind reef framework materials, does not occur and rates of bioerosion are the highest measured for any reef in the world (Manzello et al., 2008). The skeletal densities of *Porites lobata* in the southern islands are among the lowest ever documented for this species (Manzello et al., 2014). Conversely, in the northern islands, the skeletal densities of massive *Porites* are within the normal range measured across the Indo-Pacific, carbonate cement abundances are among the highest measured in the eastern Pacific, and bioerosion rates are greatly reduced (Lough, 2008; Manzello et al., 2014; Glynn et al., 2015, 2017a, 2017b). The low Ω_{arag} and high nutrients of the southern islands interact to drive these patterns, creating an unfavorable environment for the preservation of CaCO_3 .

Interestingly, values of Ω_{arag} where the sole remaining reef (Wellington Reef) persists today in Galápagos were identical to the critical Ω_{arag} value of 3.3 that was experienced by all reefs prior to the industrial revolution (Hoegh-Guldberg et al., 2007). Manzello et al. (2014) suggested there may be a CO_2 tipping point of $\Omega_{\text{arag}} = 3.0$ whereby coral reefs lose resilience to warming events because reefs in the ETP that exist above this value have exhibited recovery since the 1982–83 ENSO, whereas those in the southern Galápagos have not. Modeled Ω_{arag} values at Devil's Crown coincident with the 1982–83 ENSO were 3.01 (Fig. 7). While many factors come into play and the concept of a CO_2 tipping point for reefs is debatable (see discussion in Manzello et al., 2014), the fact that Ω_{arag} values of 3–3.3 have repeatedly been identified by different researchers, based on modeling and empirical data, suggests this is a benchmark worth tracking for reefs globally. Oceanic waters around Darwin Island will reach $\Omega_{\text{arag}} = 3$ when atmospheric CO_2 reaches 437 ppm (~ 2040) (Fig. 7). Based on the rate of increase of atmospheric CO_2 over the past 10 years (range of $1.6\text{--}3.0 \text{ ppm yr}^{-1}$ from 2007 to 16; NOAA ESRL, 2017), Darwin will experience these conditions between the years of 2026 and 2035. In the absence of CO_2 emission reductions, the warming and acidification that is projected to eliminate coral reefs from the Galápagos Islands will likely occur for nearly all reefs globally by mid-century (van Hooidonk et al., 2014).

13. Coral population recovery at Devil's Crown

13.1. Overview

Research on coral populations in the Galápagos Islands was initiated by Wellington (1975) who produced a report for the Galápagos National Park describing reef structures at Devil's Crown (Onslow Island or Corona del Diablo) and Champion Island. These two islets are located on the north coast of Floreana Island in the southern-most part of the Archipelago (Fig. 1). Glynn and Wellington (1983) later surveyed coral reefs and coral communities throughout the Archipelago with more detailed descriptions of corals at Devil's Crown. Extensive coral bleaching and mortality occurred during and following disturbances associated with the 1982–83 ENSO, eliminating over 95% of scleractinian corals in the Galápagos Islands (Glynn, 1988a). Despite these ENSO-related impacts, and nearby cool-water shoaling (Feingold,

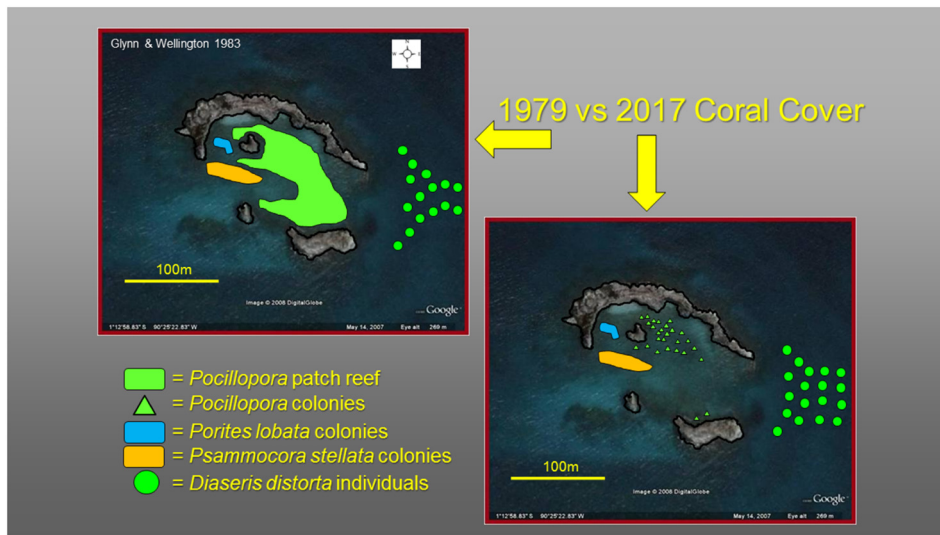


Fig. 8. Distribution of coral communities at Devil's Crown from surveys conducted in 1979 (Glynn and Wellington, 1983) and 2017 (Feingold, unpub. Data). Survey results overlay a recent (2007) Google Earth image.

1995), corals have persisted at Devil's Crown. Here we document long-term coral recovery and population trajectories from the earliest reports to the present.

There are four distinct coral communities within and adjacent to the barely emergent volcanic cone of Devil's Crown (Fig. 8). Its picturesque elliptical rim is approximately 180 × 130 m in diameter and surrounds a shallow (< 3 m depth) carbonate rubble and sediment-covered basin with a basalt substratum. Openings in the rim allow a predominantly westward current to flow through the southern portion of the basin, with a quasi-protected embayment in the northern sector. This embayment supports a recovering scattered population of *Pocillopora* spp. (Fig. 9a), and a temporally stable aggregation of large (~0.5–1 m diameter) *Porites lobata* colonies (Fig. 9b). The western portion of the channel within Devil's Crown, to the south of the embayment, supports a high-density recovered community of the free-living, stubby-branching coral *Psammocora stellata* (Fig. 9c). This species is also observed in much lower abundance scattered among the recovering *Pocillopora* spp. colonies. The deeper (13–34 m depth) eastern flank of the cone supports a free-living coral community primarily composed of the

fungiid coral *Diaseris distorta* (Fig. 9d). Interspersed among the *D. distorta* within the western border (approximately 13–15 m depth) of this community are free-living colonies of *Psammocora stellata* and a nearly extirpated population of another fungiid species, *Cycloseris curvata*. Other scleractinian coral species present at Devil's Crown, though at low abundances, include *Pavona clavus*, *Pavona gigantea* and the azooxanthellate species *Tabastraea coccinea*.

13.2. *Pocillopora* spp.

In the first benthic surveys of Devil's Crown, Wellington (1975) observed that the shallow (< 3 m depth), enclosed basin was mostly covered with an extensive thicket of predominantly *Pocillopora elegans*. However, pocilloporid corals were completely eliminated at that location (pers. obs.) during the 1982–83 ENSO event, primarily from mortality associated with anomalously warm water conditions (Glynn, 1988a, 1990). The pocilloporid reef structures reported in these early surveys subsequently disappeared following intensive bioerosion by the sea urchin *Eucidaris galapagensis* (Glynn, 1988b).

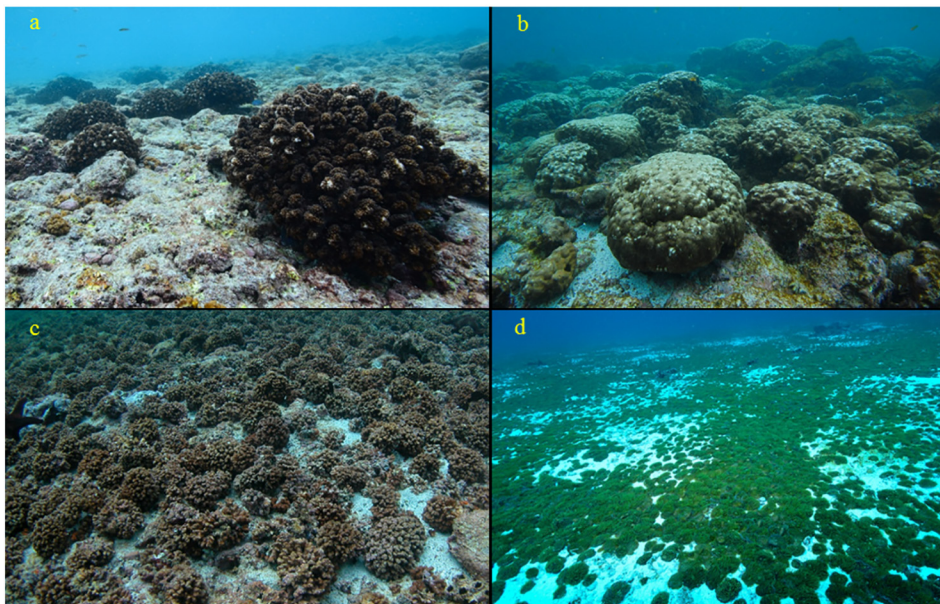


Fig. 9. Four coral communities at Devil's Crown, Galápagos Islands, Ecuador. (a) Attached, scattered colonies of *Pocillopora elegans* at the site of the former pocilloporid reef (1.5–2 m depth, 20 May 2017). Colony in foreground is approximately 25 cm in diameter. (b) Attached colonies of *Porites lobata* on basalt substrate. These colonies have persisted at this location in the NW sector of the basin since early surveys in 1975 (~2 m depth, 10 June 2011). Large colony in foreground is approximately 75 cm in diameter. (c) Free-living colonies of *Psammocora stellata* in the channel on coral sand/rubble substrate (~3 m depth, 10 June 2007). Colonies in foreground are approximately 5–10 cm in diameter. (d) Free-living individuals of the fungiid coral *Diaseris distorta* on the eastern flank of the emergent volcanic rim (~15 m depth, 11 June 2012). Largest individuals are 4–5 cm, maximum diameters.

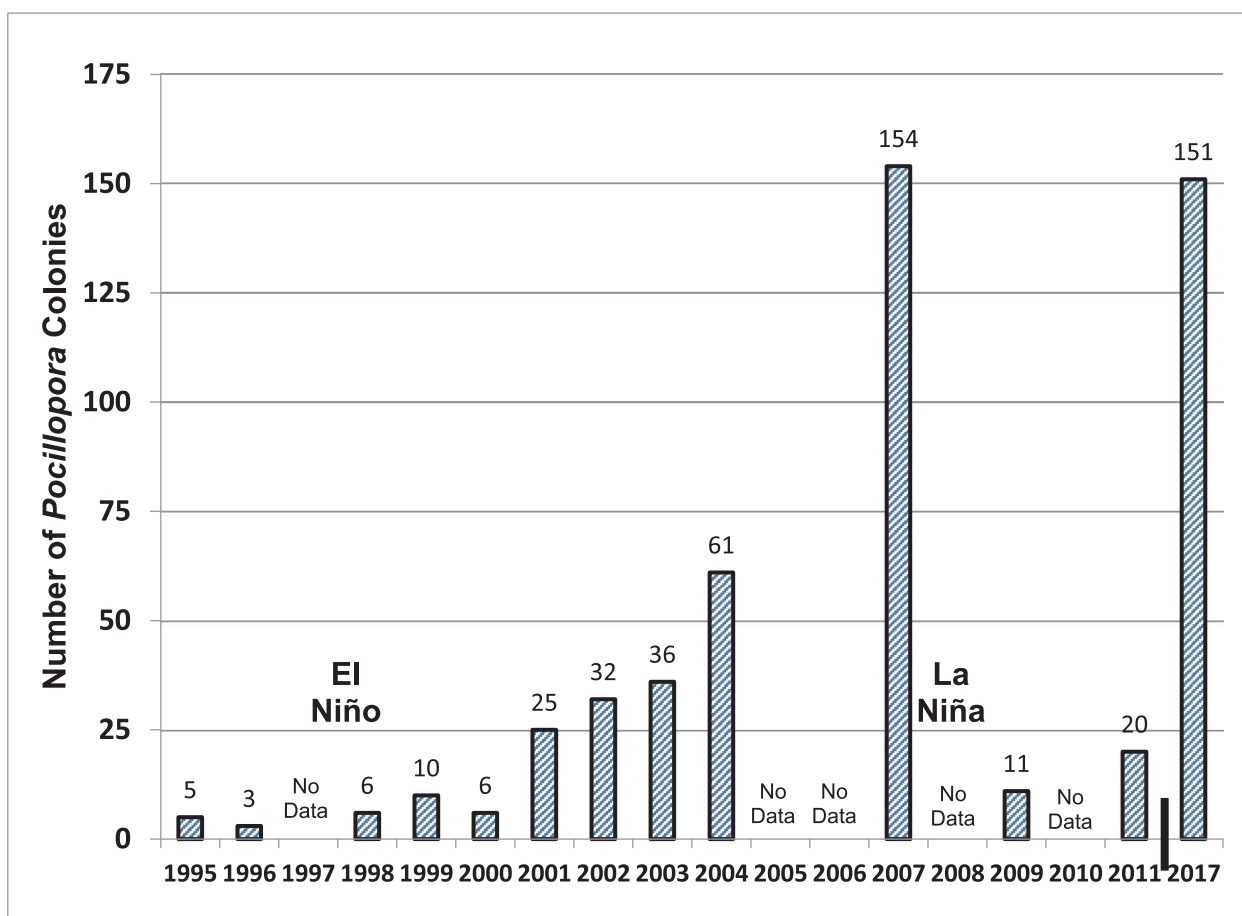


Fig. 10. Numbers of *Pocillopora* spp. colonies within the basin of the emergent basalt rim of Devil's Crown. Surveys were performed in May–June of each year. An El Niño event occurred in 1997–98 and a La Niña event occurred after the 2007 survey. Note sampling hiatus from 2011–2017.

Visual surveys within and around Devil's Crown for *Pocillopora* spp. recruitment were initiated in 1991. These were performed annually through 2004, and thereafter on a biennial or longer sampling schedule through 2017 (Fig. 10). All putative *Pocillopora* species were included in surveys as there is uncertainty about species-level taxonomic boundaries (Pinzón, 2016). Twelve years after their extirpation from this site in 1983, five colonies were observed in 1995. This population slowly increased for 12 more years, with 154 colonies of predominantly *Pocillopora damicornis* observed in June 2007. The next survey was performed two years later in June 2009, and only 11 colonies had survived. Anomalous cooling associated with the 2007 La Niña event was hypothesized as the factor responsible for this decline. In early October 2007 surface seawater temperatures dipped below 18.0 °C for 11 days, as documented by data loggers deployed in situ at ~2 m depth, and a minimum temperature of 16.8 °C was recorded. In six years of previous seawater temperature data from this same location, recorded temperatures were only twice (for a one hour period each time) below 18.0 °C. The coral population increased to 20 colonies in 2011, and then after a six year survey hiatus, 151 colonies of predominantly *Pocillopora elegans* were observed in 2017 (Fig. 9a). The coral population increase between 2001 and 2007 (+129 colonies) is nearly identical to that from 2011 and 2017 (+131 colonies).

The predominance of one type of *Pocillopora* species is consistent with this taxon's capacity to reproduce asexually by fragmentation. In some cases this mode of reproduction results in populations of only one genotype (Baums et al., 2014), and although genetic sampling has not been performed on colonies at Devil's Crown, a clonal-predominant species is consistent with this asexual model. In the absence of further environmental stress, it is projected that continued recovery will occur

with the potential of reforming an incipient patch reef.

13.3. *Porites lobata*

A large aggregation of *Porites lobata* in the northwest quadrant of Devil's Crown (Fig. 9b) has persisted from the 1970s (Wellington, 1975) until the present through at least two severe ENSO-associated warming events (1982–83 and 1997–98) and one strong cooling event (2007–08). These colonies are the largest (115 cm major axis) currently alive in the southern and central Archipelago (Fig. 5). Photo quadrats performed on 17 colonies from 1993 through 2011 documented small, non-significant tissue area increases. Bleaching and partial mortality were observed during anomalous cooling below 20.0 °C for 124 days during 2009 (Paul, 2012). The resilience demonstrated by this community suggests it will persist in the future.

13.4. *Psammocora stellata*

A dense aggregation of free-living *Psammocora stellata* was reported by Glynn and Wellington (1983) in the western sector of the channel that bisects the southern part of the enclosed basin of Devil's Crown. This channel is the deepest part (~3 m depth) of the enclosed basin. The *P. stellata* population disappeared following disturbances associated with the 1982–83 ENSO. It was hypothesized that anomalously strong surface waves from an atypical direction (Robinson, 1985) displaced these unattached colonies. Recovery began in the early 1990s, and by the mid-2000s colonies were abundant again in their former habitat (Fig. 9c). Resistance of *P. stellata* colonies to ENSO-associated warming (Feingold, 1995) and their ability to rapidly reproduce through asexual

fragmentation suggests that they will persist at this and other locations in the Galápagos Islands (Feingold, 2001).

13.5. *Diaseris distorta* and *Cycloseris curvata*

Devil's Crown is the only known location of living fungiid corals in the Galápagos Archipelago. An extensive population of *Diaseris distorta* individuals is present on sand and rubble substrata on the eastern flanks of the cone to a distance of approximately 1 km and 34 m depth. Population densities are greatest closer to the cone in depths of 13–20 m, with over 100% cover commonly observed (Fig. 9d). Within this western sector of the community, scattered colonies of *Psammocora stellata* and another fungiid, *Cycloseris curvata*, occur. While the *D. distorta* population is estimated to be over 500,000 individuals (densest aggregations are ~ 2000 individuals m^{-2}) (Feingold, 1995), there was only one individual of *C. curvata* observed in May 2017. Its highest population size was over 200 individuals in the mid-1990s.

Persistence of high numbers of *D. distorta* are likely due to a combination of factors: the capacity of asexual reproduction via autotomous fragmentation (Yamashiro and Nishihira, 1998), resistance to bleaching-induced mortality and the mitigating effects of cooler conditions during ENSO warming in its deeper habitat (Feingold, 2001). Therefore, *D. distorta* continues to be a robust and common component of the deeper benthos to the east of Devil's Crown, whereas *C. curvata* is in critical danger of extirpation from the Archipelago.

13.6. Summary

Devil's Crown was a focal point of coral studies in the earliest surveys by Wellington (1975), and it continues to attract attention by researchers due to ongoing dynamic processes of impact and recovery. Four enduring coral communities at Devil's Crown are each primarily composed of four different coral species that continue to contribute to benthic structural complexity, increasing species diversity compared to barren adjacent habitats. The Galápagos Islands present marginal habitat for coral survival, and these perennial communities are a testament to the resilience of certain coral species at this southerly location within the Archipelago.

14. Projected condition of the Wellington Reef

Located on the northern-most island (Darwin), Wellington Reef (WR) is presently the only known coral reef in the Galápagos Islands. It has demonstrated cycles of disturbance and recovery over the past 30 years of study, but has persisted. In contrast to WR, coral mortality in the central and southern islands was followed immediately by intensive bioerosion due primarily to *Euclidaris galapagensis*, an important echinoid corallivore in the eastern tropical Pacific, which ultimately resulted in the conversion of reef frameworks into rubble and sand sediments, forming substrata suitable for rhodolith bed formation (Halfar and Riegl, 2013; Glynn et al., 2015). In a modeling study, Glynn et al. (2017a, 2017b) evaluated the hypothesis that WR will not be able to recover to pre-disturbance levels of live coral cover when projecting the state of the reef 50 years into the future, given “business as usual” eastern Pacific ENSO disturbances that cause significant coral bleaching, mortality and subsequent bioerosion by *E. galapagensis*.

The modeling study suggested that the recovery potential of WR will decrease with an increase of *E. galapagensis* population density (Fig. 11). The hypothesis that WR will not be able to recover to empirically determined 2007 live coral levels was validated, given that at the lowest mean echinoid density ($\bar{x} = 0.9$ ind m^{-2}) the mean recovery potential was 68.2%. This result was unexpected in light of the robust recoveries observed at coral sites in the northern Galápagos Islands following four ENSO disturbances, from 1982–83 to 1997–98 (Glynn et al., 2009, 2015, 2017a, 2017b). Even with over 42.5% of test runs at the lowest mean echinoid density ($\bar{x} = 0.9$ ind m^{-2}) at or exceeding a 100%

recovery potential, the overall mean recovery potential of 68.2% was well below the target of 100%. This result may be explained by the fact that a full recovery requires sufficient time between successive bleaching events to enable surviving *Porites lobata* coral colonies to regenerate live tissue cover, and for recruits to settle and grow to sexual maturity.

Given the current population densities of *E. galapagensis*, reef framework accretion is expected to continue for several decades into the future. If *E. galapagensis* population densities should increase, for example due to overfishing, i.e. depletion of echinoid predators (Ruttenberg, 2001; Sonnenholzner et al., 2009; Edgar et al., 2010, 2011) or changing environmental conditions such as increased upwelling and elevated nutrients (Feldman et al., 1984; Chavez and Brusca, 1991; Witman and Smith, 2003), echinoid recruitment and growth could result in densities of 8–10 ind m^{-2} or higher. Under these conditions, reef accretion could switch to a mode of degradation. Beyond the difficulty of predicting ENSO activity and subsequent *E. galapagensis* bioerosive impacts, a multitude of other potential stressors, such as lowered aragonite saturation state, rising sea level, coral diseases and invasive species, add to the uncertainty of forecasting the fate of WR. Clearly, the significant decrease in recovery potential as a function of increased echinoid density suggests that a line of action with a high probability of success, at least into the near future, is maintaining and enforcing the marine protected area (MPA) status of the northern Galápagos Islands, preventing over-exploitation of echinoid predators.

15. Climate and conservation

Given that recent strong ENSO warm phase events (Fig. 3a) evidenced broad equilibrium shifts in marine communities, as well as probable marine species extinctions (Edgar et al., 2010), the Galápagos Islands case can help assess species resistance and resilience with insight into understanding of ecosystem response to mid to long-term climate change scenarios (albeit at different scales). Concerns notably include ocean acidification (see Section 12 above) under climate change forcing, more abrupt and intense ocean state transitions between seasons and reduced recovery periods for species between strong ENSO events (Hughes et al., 2018), and any prolonged suppression of Equatorial Undercurrent upwelling impacting local production. As with the terrestrial realm, there is an increased window of opportunity and displacement potential for marine invasive species establishing and propagating via maritime traffic between well-frequented ports.

While ENSO climate trends for the future are still unknown (Vecchi and Tittenberg, 2010), the known range of ocean conditions have important compounding interactions with the in-shore fisheries and tourism activities that have proliferated under urban population growth since the 1960s. Many such pressures can be alleviated to mitigate climate related risks; e.g. through low impact anchorage sites, responsible dive tourism, ecologically sustainable well dimensioned fisheries, re-settlement programs and protected coral nurseries for local fisheries.

Conversely, broader ocean acidification and basin-scale circulation shifts into the future being beyond the jurisdiction of local authorities is an international concern with direct implications for local ecosystem health and human well-being. Although conserving and encouraging natural climate resilience while considering the suite of anthropogenic needs and impact of stressors is an ongoing challenge for conservation research and Galápagos Marine Reserve management, twinning global climate solutions with local observations, accountability and impact is likely important for resolution of climate trends. Elucidating the influence of basin level ocean signals at small scales is of direct relevance for local conservation of the Islands' remarkable natural heritage, resilience of tourism and fisheries economies, and research and learning opportunities.

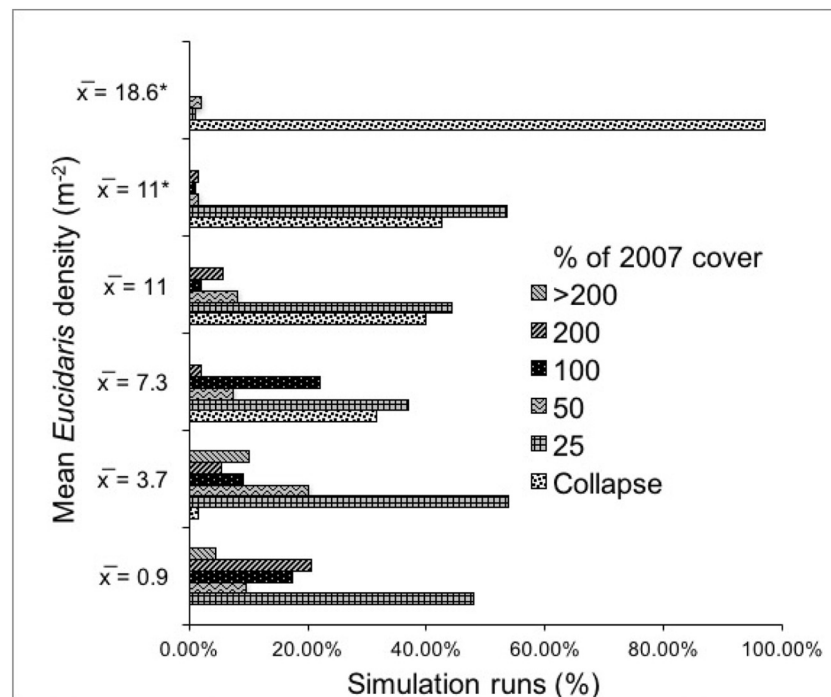


Fig. 11. Recovery responses for *Eucidaris* densities ranging from very low to very high. Asterisks denote echinoid densities of 11.0 and 18.6 ind m⁻² assuming 24-hr grazing. Modified after P.J. Glynn et al. (2017a, 2017b).

16. Concluding remarks

In light of the numerous and diverse disturbances and declines in Galápagos coral populations in recent decades, protection and management of this unique biotic resource are critical. The government of Ecuador initiated several effective measures – implemented through the Galápagos National Park Service – to safeguard corals and structural reef frameworks across the Archipelago. Key international and national developments towards this end have been the designation of the Galápagos Islands as a World Heritage Site in 1978 by UNESCO, and the establishment of the expansive (~133,000 km²) Galápagos Marine Reserve in 1998 (Denkinger and Vinueza, 2014). Also, the area surrounding the northern Galápagos Islands and several other smaller areas in the central and southern Archipelago, became a marine sanctuary (no take zone) in 2016.

To monitor the health of coral ecosystems, comprehensive baseline surveys of the occurrence and condition of coral communities were performed across the Archipelago by teams of biologists from the Charles Darwin Research Station (Danulat and Edgar, 2002). It is essential that these surveys continue in order to allow for quick recognition and mitigation of potentially damaging stresses such as coral bleaching, diseases, invasive species, overfishing, bioerosion, inter alia. In areas of abundant live coral cover, coral species needing continuing protection, and recovering coral populations should be more strictly protected. This is accomplished via exclusion zones for tourism and fishing. Entry to such areas for scientific and management purposes is also strictly controlled. The collection of corals is prohibited except for well-defined and justified research purposes. In order to prevent anchor damage to corals, a new system of permanent moorings was introduced to the Islands (Merlen et al., 2009). Existing and future measures to control and regulate artisanal, commercial and sport fishing activities are crucial in order to limit direct and indirect impacts of overfishing on coral condition. It is our hope that current interest and commitment in protecting coral resources, and the biodiversity they enrich, continue in the Galápagos Islands.

As a significant natural resource for both its aesthetic qualities and key role in ecosystem function, it is important to preserve the corals of

the Galápagos Islands. This can be achieved through education, particularly of tourists who visit these diverse and attractive habitats.

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