

# Coral reef recovery in the Galápagos Islands: the northernmost islands (Darwin and Wenman)

Peter W. Glynn · Bernhard Riegl · Samuel Purkis ·  
Jeremy M. Kerr · Tyler B. Smith

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**Abstract** The remote northernmost Galápagos Islands, Darwin and Wenman, exhibited well-developed coral communities in 1975, which were severely degraded during the 1982–1983 El Niño warming event. Mapping of the coral reef at Darwin, herein Wellington Reef, shows it presently to be the largest known structural reef in the Galápagos. It consists of numerous 1- to 3-m-high *Porites* framework towers or stacks and overlies a carbonate (coral/calcareous sediments) basement. Pre-disturbance Wellington Reef was constructed chiefly by *Porites lobata* and *Pocillopora elegans*, and Wenman coral cover was dominated by *Pavona clavus* and *Porites lobata*. Subsequent surveys in 2012 have demonstrated robust recovery in spite of ENSO thermal shock events, involving both high and low stressful temperatures that have caused tissue bleaching and mortality. No losses of coral species have been observed. Radiocarbon dating of 1- to 3-m-high poritid framework stacks, from their peaks to bases,

revealed modern ages of up to 690 yr. Incremental stack growth rates ranged from 0.15–0.39 to 1.04–2.40 cm yr<sup>-1</sup>. The former are equivalent to framework accretion rates of 1.5–3.9 m Kyr<sup>-1</sup>, the latter to coral skeletal growth rates of 1.0–2.4 cm yr<sup>-1</sup>. Coral recovery in the central and southern Galápagos has been nonexistent to low compared with the northern islands, due chiefly to much higher population densities and destructive grazing pressure of the echinoid *Eucidaris galapagensis*. Thus, coral reef resistance to ENSO perturbations and recovery potential in the Galápagos are influenced by echinoid bioerosion that varies significantly among islands.

**Keywords** Galápagos coral recovery · Reef accretion · ENSO thermal bleaching · Echinoid bioerosion

## Introduction

During the past few decades, from the early 1980s, many studies have reported on the global-scale decline of coral reefs (e.g., Hoegh-Guldberg 1999, 2012; Wilkinson 1999, 2008; Jackson et al. 2001; Hughes et al. 2003; Pandolfi et al. 2003; Bruno and Selig 2007). Loss of living coral cover and degradation of coral reef formations have occurred in all tropical and subtropical biogeographic regions due to multiple causes, with coral bleaching (Wellington and Glynn 2007; Baker et al. 2008; van Oppen and Lough 2009) and diseases (Harvell et al. 1999; Porter 2001; Rosenberg and Loya 2004) among the prominent drivers. Both direct and indirect effects are contributing to reef decline, with over-fishing, eutrophication, and storms also exacerbating reef decline. In spite of this precipitous decline, the majority of monitored coral reefs in all major regions, except for the western Atlantic (Greater

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P. W. Glynn (✉)

Department of Marine Biology and Ecology, Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, FL 33149, USA  
e-mail: pglynn@rsmas.miami.edu

B. Riegl · S. Purkis · J. M. Kerr

Oceanographic Center, National Coral Reef Institute, Nova Southeastern University, 8000 North Ocean Drive, Dania, FL 33004, USA

T. B. Smith

Center for Marine and Environmental Studies, University of the Virgin Islands, #2 John Brewers Bay, St. Thomas, VI 00802, USA

Caribbean, Roff and Mumby 2012) have demonstrated some level of recovery.

Eastern Pacific coral reefs, particularly at equatorial locations, suffered severe bleaching and high rates of mortality, due chiefly to anomalous high sea temperatures that accompanied the 1982–1983 El Niño event (von Prah 1983, 1985; Cortés et al. 1984; Glynn 1984; Robinson 1985). Corals in the Galápagos experienced the highest overall mortality in the equatorial eastern Pacific (EEP). Of 14 surveyed reefs, mean coral mortality was 97 %, and some reefs in the southernmost islands experienced 100 % coral mortality (Glynn et al. 1988). The positive SST anomalies and rate of temperature increase were the greatest observed in the EEP region. Coral mortality in the central and southern islands was followed immediately by intense bioerosion (Glynn 1984, 1990, 1994), due chiefly to motile, externally grazing sea urchins (*Eucidaris galapagensis*) in high abundance. The intensity of sea urchin grazing on dead, algal-coated corals resulted in the conversion of reef frameworks into rubble, rhodolith, and sand sediments (Halfar and Riegl 2013).

Coral mortality was also high in the northernmost Galápagos, but due to the remoteness of this area it was not surveyed with regularity (Fig. 1a–c). Robinson (1985) noted that at Wenman in December 1983, at least 90 % of corals to 30 m depth were bleached and covered with algae. Darwin was not re-surveyed until 1992, 9 yr after the bleaching disturbance, to depths of 30 m. Much of the reef frame remained intact (Glynn 1994). Later investigations showed continuous increases in coral cover (Glynn et al. 2009).

To help evaluate the recovery status of the Darwin Island Reef, we here examine (a) temporal changes in live coral cover (1975–2012), (b) the depth distribution of potential framework structures, (c) the vertical heights and estimated ages (radiometric C-14 dating) of reef frameworks, and (d) the population sizes of bioeroding echinoids. The results of this analysis are compared and contrasted with the lack of reef recovery in the central and southern Galápagos.

## Materials and methods

### Oceanographic setting, coral fauna, and island study sites

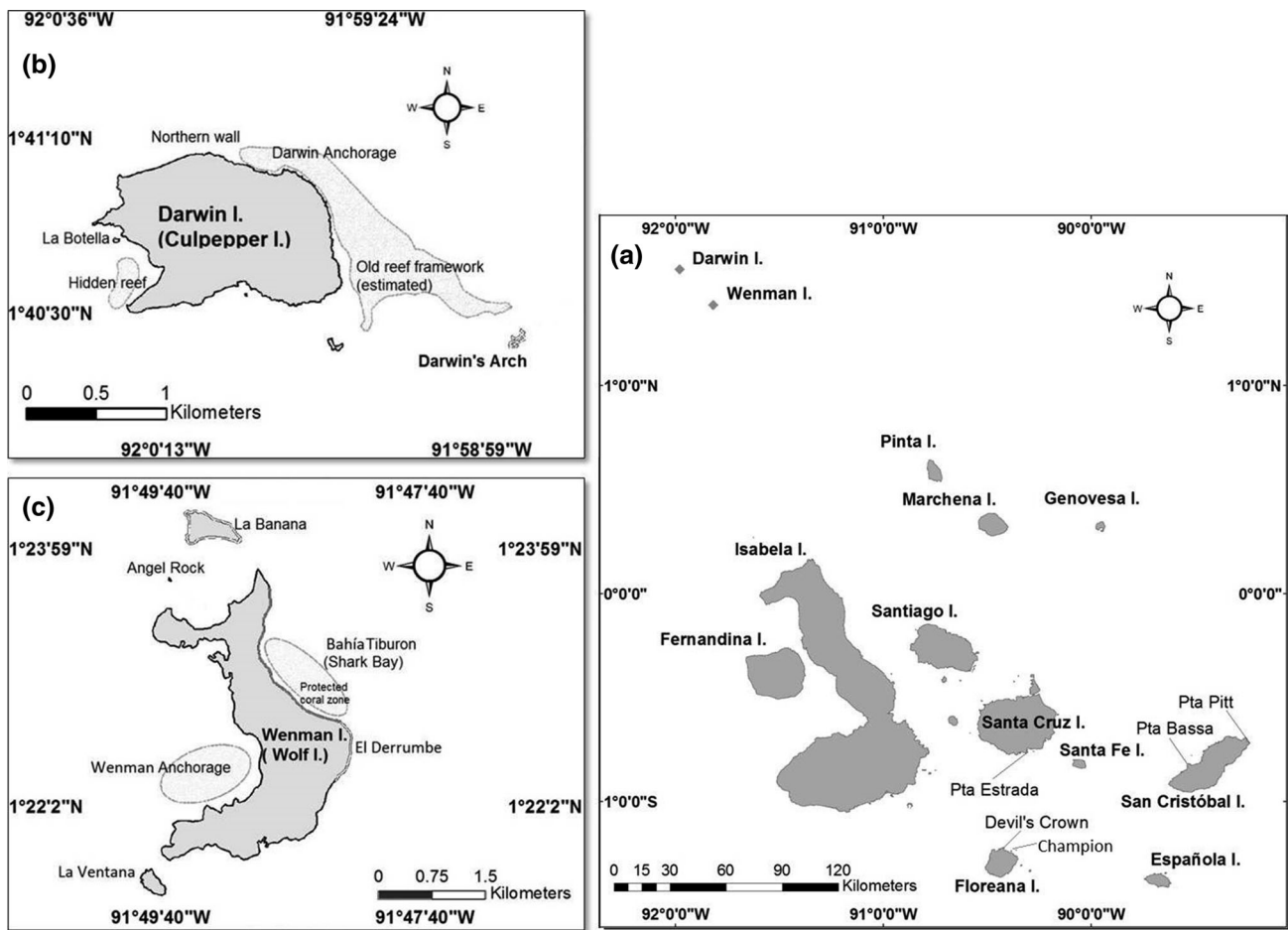
Darwin (Culpepper) and Wenman (Wolf), located astride the Equatorial Front, are bathed by waters 2–3 °C warmer on average than the central and southern islands (Banks 2002; Fiedler and Talley 2006). The zooxanthellate coral fauna of the Galápagos, both the northern and southern islands, is species poor. Hickman (2008) lists 21 species

and to this may be added *Porites evermanni*, recently discovered at Darwin (Boulay et al. 2014). Reef building is performed primarily by *Porites lobata*, *Pavona clavus*, *Pocillopora elegans*, and *Pocillopora damicornis*. Since *Porites lobata* and *Porites evermanni* could not be distinguished with confidence in the field, it is possible that the latter contributes more to coral community cover than reported here. Other species of *Pocillopora*, *Pavona*, *Gardineroseris*, *Psammocora*, and *Leptoseris* are common to rare; *Cycloseris* and *Diaseris* do not typically occur in shallow coral communities.

Darwin and Wenman are the northernmost islands in the Galápagos Archipelago (Fig. 1b, c) and have been the subject of a previous study by the authors (Glynn et al. 2009). The islands have been investigated since 1975, when only briefly described (Glynn and Wellington 1983), but studied in more detail from 1992 to 2012. Particular attention is given to the spatial extent and structure of the coral reef at Darwin, presently the largest, actively accreting reef in the Galápagos. Henceforth, this reef is named Wellington Reef, in honor of Wellington (1975) who pioneered efforts to establish marine protected areas in the Galápagos. The data series for the present study consists of coral-level (size distribution, estimation of live tissue cover) measurements (2000, 2007, and 2012), measurements of framework height (1992, 2000, 2006, 2007, and 2012), and phototranssects (2007 and 2012). Comparative observations and data from central (Pinta) and southern island study sites (Bartolomé, Santa Cruz, Santa Fe, San Cristóbal, Floreana, and Española) are included from field studies in 1975–1976 and over several years to 2012.

### Reef bathymetry

To describe the structural complexity of Wellington Reef, vertical measurements of framework structures were made in situ. A continuous carbonate framework exists, consisting of coral-built towers in various stages of lateral fusion. These towers, referred to as stacks, are constructed predominantly by *Porites lobata* with occasional associated agariciid (*Pavona*) and pocilloporid species. Heights of 54 stacks between 12 and 16 m depths were measured in 2012, from their bases (adjacent to the carbonate substrata from which they arise) to their tops. Some stacks had already been measured in earlier years (Table 1). To obtain a clear overview of the three-dimensional structure, a bathymetric image was produced. Tidally corrected acoustic depth soundings were obtained across the reef from which the relationship to RGB pixel values on a WorldView-2 satellite image was determined. Using the derived algorithm, a pseudo-bathymetry that was subsequently corrected against known depth ground-truthing



**Fig. 1** a Galápagos study sites and views of landmarks at northernmost **b** Darwin and **c** Wenman. Wellington Reef location at Darwin is on ‘old reef framework’ patch, and coral community study site in Shark Bay is in ‘protected coral zone’

**Table 1** *Porites* stack heights measured over a 20-yr period in the western/central sectors of Wellington Reef, Darwin Island

Sampling year	N	Mean ( $\pm$ 1 SD)	Range
1992	5	2.46 (0.32)	1.8–3.4
2000	4	3.68 (1.25)	2.0–5.0
2006	6	2.58 (0.44)	1.0–4.0
2007	15	1.97 (0.44)	1.4–2.7
2012	37	2.24 (0.59)	1.2–3.7

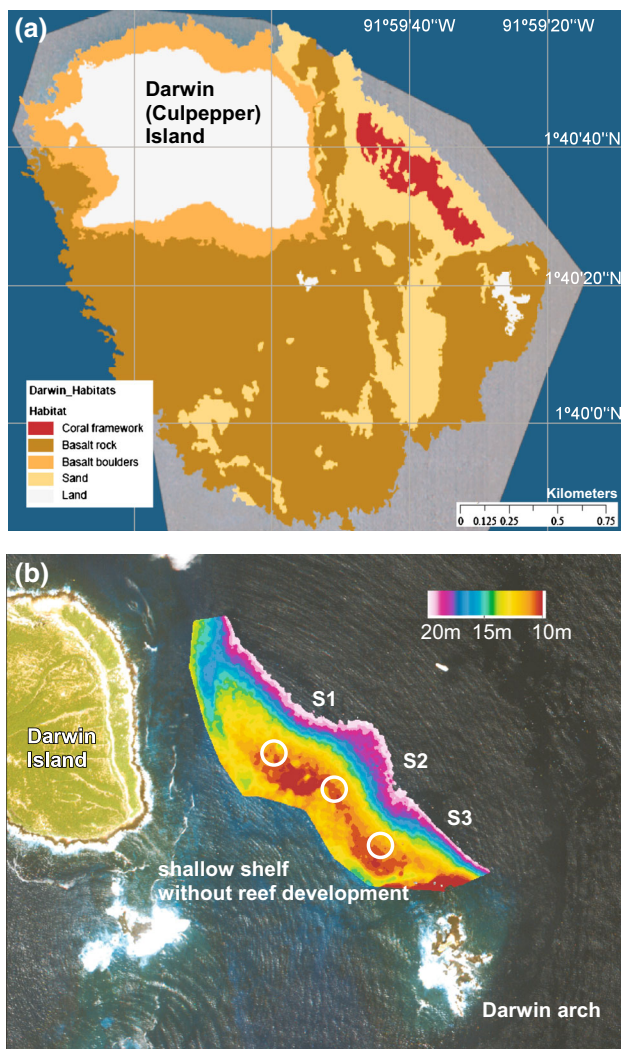
Measurements are in meters and biased toward the higher elevations encountered in the sampling area

points was obtained across the entire reef. Major habitat types were differentiated by color values on the satellite image (Fig. 2a). At Wenman, few continuous incipient frameworks within which several coral-built structures amalgamate are present; framework height measurements refer in most cases to the heights of large individual coral colonies. One hundred and twenty-two of these were

sampled over a depth range of 6–34 m. These corals grow in a habitat characterized by large basalt boulders, derived from the steep island coastline, on a steeply descending slope. This habitat imposed severe restrictions on the optical resolution of the isolated corals, and a bathymetric image of the coral structural contribution to the landscape, comparable to that at Darwin, could not be achieved from remote sensing.

**Radiocarbon dating**

In order to determine ages and growth rates of Wellington Reef framework stacks, coral (*Porites*) samples were collected at varying distances from the tops to the bases and subjected to radiocarbon dating analysis. Dates were calibrated using Calib 6.0 software (Stuiver and Reimer 1993; Stuiver et al. 2005). No historical reservoir corrections are available for the Galápagos; therefore, average modern reservoir corrections for nearby Santiago Island (Taylor and Berger 1967) were used to calibrate dates for



**Fig. 2** Views of Wellington Reef based on bathymetry extraction from WorldView-2 satellite imagery. **a** Location of reef (burgundy) in relation to carbonate sand patches and surrounding basalt substrate types. **b** Color-coded carbonate buildups over a 10–20 m depth range between Darwin's Arch and east Darwin shore. Circles on reef denote locations of sampling sites S1–S3

Darwin. However, since overall oceanographic conditions between Santiago and Darwin may well differ significantly, in particular with reference to frequency and severity of upwelling, we also report data corrected for the normal tropical ocean reservoir. Significant differences in biological structure of benthos indicate that Darwin and Wenman support more tropical biota than the southern islands (Bustamante et al. 2002; Edgar et al. 2002).

#### Coral surface cover and condition

Live coral cover was quantified at Darwin on May 21–23, 2007, and June 4–8, 2012, from 15-, 10-m-long transects each consisting of 10 photographs (150 total) of 0.25 m<sup>2</sup>

quadrats laid at predetermined random locations. Three sets of five transects, each perpendicular to the long axis of Wellington Reef and separated by 5 m, were completed at three principal sampling sites (S1–S3; Fig. 2b) separated by 250–300 m. Corals in the photographs were digitized and color coded by genus. From these images, the areal cover by coral taxa was calculated. Repeated sampling among years is not based on exact locations, but rather on closest possible proximity to sampling sites from previous years. It is illegal to affix visible (or any) markers to coral communities in the Galápagos Marine Reserve.

Coral cover at depth intervals was determined at Shark Bay, Wenman, on January 18–19, 1975, and from June 2 to June 5, 2012. In 1975, coral cover was quantified from photo-quadrats at 5 depths to 30 m [transect site in Glynn and Wellington (1983), Fig. 42, Wolf or Wenman]. In 2012, haphazard initial dive locations were spread within a kilometer across Shark Bay. At each location, transects were laid parallel to the isobath in zones 9–15, 16–25, and 26–32 m; however, not all depths were sampled at each location. Details for video transects are in Smith et al. (2013). Transects were taken at 15 consecutive video still captures and were approximately 8 m in length. The substrate of each captured image was identified under 15 randomly placed points (Kohler and Gill 2006) for abiotic substrate, and sessile animal and plant species to the highest possible taxonomic resolution. Images were pooled to provide one estimate of coverage for each substrate category on each transect. Overall, 34 replicate transects were assessed.

Long-term data on live coral cover in the central and southern Galápagos, along with sampling site locations and chain transect and photo-quadrat sampling methods, are available in Glynn and Wellington (1983), Glynn (1994), Glynn et al. (2001), Wellington and Glynn (2007), and Baker et al. (2008).

During the surveys in 2000, 2007, and 2012, heights and diameters of *Porites* colonies first encountered on Wellington Reef were measured to determine population size structure of the principal reef-building coral. Percentage estimates of live and dead surface areas of each colony were also recorded. Dead surfaces were further classified as 'old dead' (OD), usually highly eroded and overgrown by algae, barnacles, and other encrusting benthos, and 'new dead' (ND), often with light-colored surfaces revealing fine skeletal structures and often with filamentous algae or thin crusts of coralline algae.

#### Echinoid abundances

At Darwin and Wenman, echinoid abundances were sampled by counting individuals in 10 × 2-m transects laid across coral frameworks perpendicular to the long axis

(NW/SE) of Wellington Reef, and in video transects at Shark Bay, Wenman (as described above). The two species targeted were *Eucidaris galapagensis* and *Diadema mexicanum*, active bioeroders in the eastern Pacific region (Glynn 1988; Eakin 2001; Alvarado et al. 2012). Other species present in the sampling areas, especially in the southern islands, were also enumerated during daylight hours. A 0.25-m<sup>2</sup> quadrat was positioned within each of the four quadrants of the 20 × 1-m<sup>2</sup> plots sampled. All visible surfaces were searched, including cavities and the accessible undersides of colonies (without colony dislodgment). Sampling in the central and southern islands was mainly with 0.25- and 1.0-m permanently marked and randomly placed quadrats on study reefs established in 1975–1976 and monitored until 2010–2012. All of these sites were sampled on multiple occasions.

Echinoid counts from visual surveys, however, provide only minimum estimates of true abundances. To obtain a measure of the abundance of cryptic echinoids associated with massive coral colonies, i.e., individuals not visible from the inspection of accessible surfaces, counts were performed of all echinoids present on the surfaces and undersides of upturned colonies. To enumerate cryptic echinoids, each coral colony was lifted and tilted to allow counts on undersides. All colonies were returned to natural positions, and monitoring of these colonies in subsequent years did not reveal any damage. This sampling was performed at Onslow patch reef on February 9, 1986, and October 29, 1987.

## Results

### Reef structure and coral cover

Wellington Reef is just less than 1 km in length (Fig. 2a, b). Bathymetric information from satellite imagery and on-site surveys shows the irregular surface of the reef, consisting of numerous coral stacks formed primarily by *Porites lobata* (Fig. 3a). There is no shallow reef flat; the shallowest areas are ~10 m deep, and depth is highly variable. The reef itself follows the seaward slope of the SE insular shelf and shows no signs of active accretion at depths >25–30 m. Most stack development occurs between 12 and 20 m depth with occasional isolated colonies of *Pavona clavus*, *Pocillopora* spp., and *Pavona maldivensis* present on the stacks or on more low-lying reef substrates. Stack heights measured over a 20-yr period (some repeatedly, others only in a single sampling period), between 12 and 16 m depth, demonstrated mean values from 1.97 (2007) to 3.38 (2000) m (Table 1). Modal stack height was ~2.5 m (Fig. 4a, b). Heights represent vertical distance above sediment or firm carbonate substrata between stacks. Reported heights do not include additional vertical heights

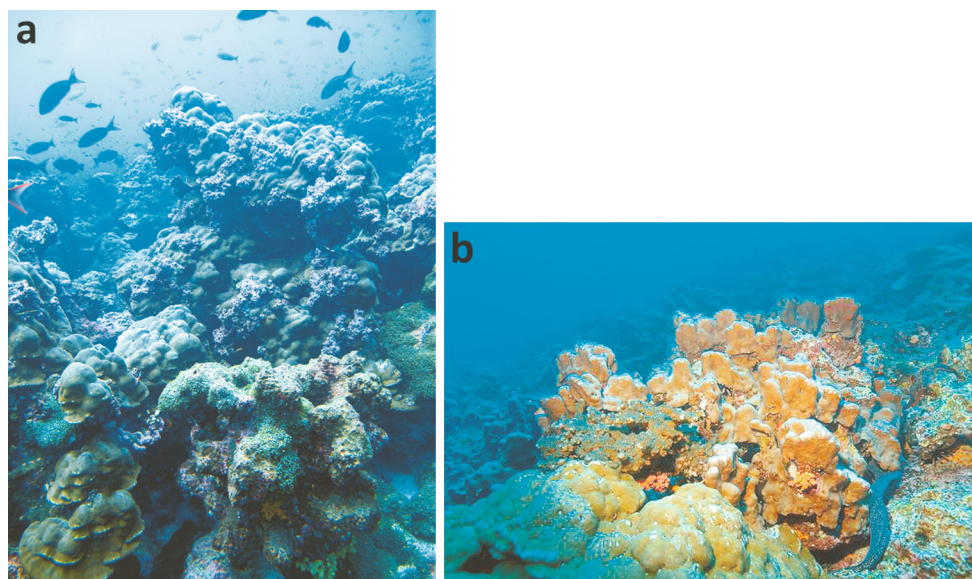
below loose sediments. Probing in basal sediments revealed a sand cover of 0.5–0.8 m above the limestone basement, which was similar across all survey depths, suggesting presence of ~4 m of coral framework. Stack heights demonstrated a significant exponential decrease with depth (Fig. 4c).

The NW half of Wellington Reef bears NE to SW oriented channels (Fig. 2a), filled with coarse, calcareous sand, and highly worn, encrusted, broken branches of *Pocillopora* spp. Low-lying (0.5–1.5 m high) *Porites lobata* frameworks are present at 20–25 m with scattered patches of *Pavona varians* and *Pavona chiriquirensis*. Small *Porites lobata* colonies (<0.5 m high) are present at the reef base, between 25 and 30 m depth, with numerous *Tubastrea coccinea* present on dead upper surfaces of poritid colonies. A gently sloping calcareous sand apron, composed of coral rubble and dead *Cycloseris elegans*, is present at 30 m and deeper.

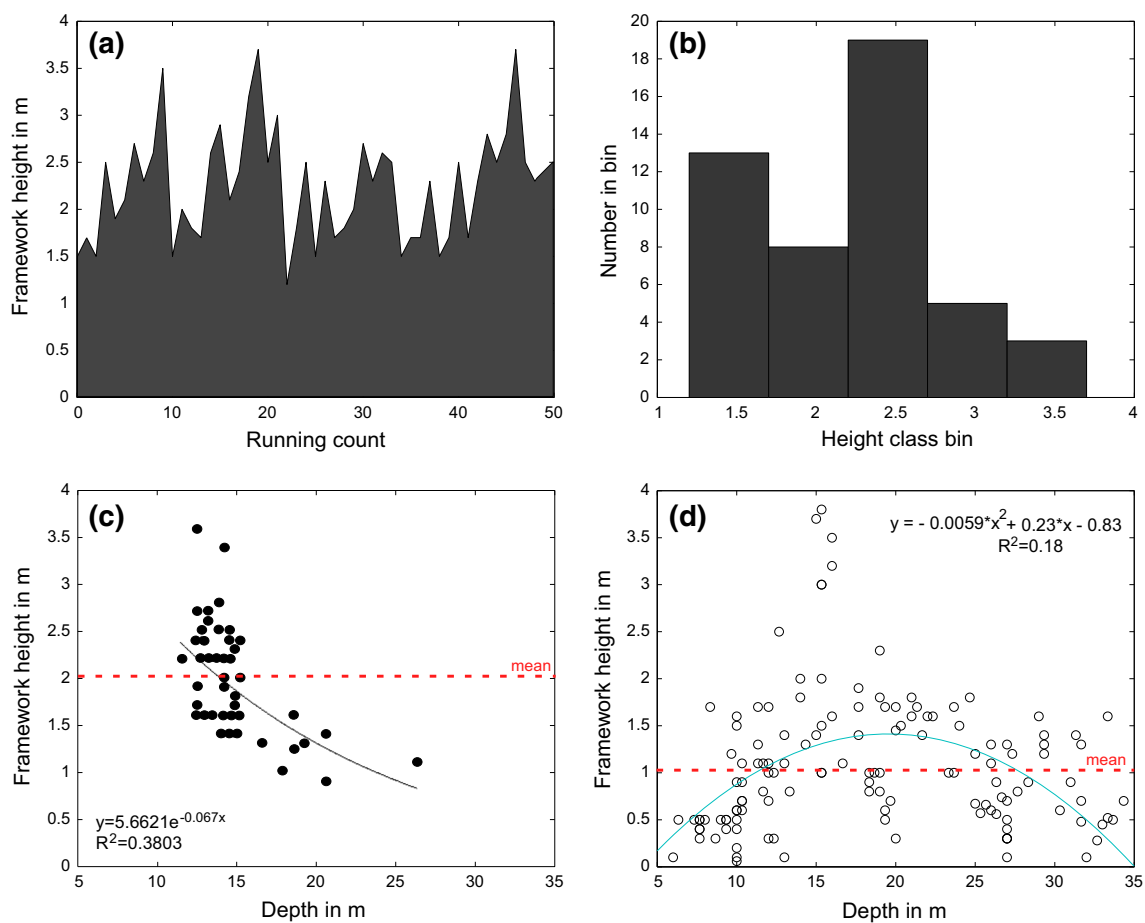
The best developed coral community at Wenman is located along the leeward NE shelf at Shark Bay (Bahía Tiburón) and is about 1 km in length (Fig. 1c). Unlike the Darwin reef, which is distant (~200 m) from the island shoreline, corals at Wenman occur a few meters from shore, in a boulder field at relatively shallow depths. *Pocillopora elegans*, *Pocillopora effusus*, and *Pocillopora eydouxi* are present as isolated colonies on the upper surfaces of basalt boulders at 5–8 m depth. *Porites lobata* predominates between 10 and 20 m, diminishing in abundance to 30 m. *Pavona* spp. occur commonly between 15 and 30 m depth. Maximum framework height at Wenman, 3.5–3.8 m, is similar to that of the Wellington Reef (Figs. 3b, 4d). However, the majority of the height measurements were of large individual colonies of *Porites lobata* and not multiple fused colonies forming coral frameworks or stacks. A weak parabolic relationship with depth is evident with large massive colonies present between 10 and 25 m depth.

Coral cover on the Wellington Reef increased significantly from 2007 to 2012 (Mann–Whitney *U* test,  $W = 8283.5$ ,  $p$  value =  $7.844e-05$ , data were non-normal and heteroscedastic, tested with Fisher's *F* and Fligner–Killeen tests). The increase was due chiefly to *Porites lobata*; the overall increase of live coral at the three sampling sites was from 19.4 to 32.3 % over the 5-yr period (Table 2).

Photo-quadrat sampling of live coral cover over a depth gradient of 7–30 m at Shark Bay, Wenman in 1975 revealed mean overall live cover of 14.4 % (SD = 8.65; Glynn and Wellington 1983). The same coral community sampled in this study in 2012, although not the identical site surveyed earlier, demonstrated significantly higher live cover (mean = 36.94 %, SD = 22.31; Mann–Whitney *U* test,  $W = 445$ ,  $p$  value 0.04, data were non-normal and heteroscedastic, tested with Fisher's *F* and Fligner–Killeen



**Fig. 3** **a** Wellington *Porites* stack at Darwin (14 October 2014, 17 m depth, courtesy V.W. Brandtneris) about 2 m high; other stacks visible in background. **b** Coral community, Shark Bay, Wenman (25 July 2007, 9 m depth, courtesy A. Hearn)



**Fig. 4** Wellington Reef stack heights, **a** as a proxy for geomorphology, the sequence of measured stacks (5–10 m apart) illustrates variability in stack height and overall framework rugosity, **b** frequency

of occurrence, **c** versus reef depth. **d** Wenman coral community colony heights versus depth. Dashed red lines in **c**, **d** denote mean framework heights

**Table 2** Comparison of Wellington Reef live coral cover ( $\pm 1$  SD) of species present in ten  $1/4 \text{ m}^2$  quadrats in each of five transects at three sampling sites in 2007 and 2012

Sample Sites	<i>Porites lobata</i>				<i>Pavona clavus</i>				<i>Tubastrea coccinea</i>				<i>Pocillopora</i> spp.				Mean cover		
	2007		2012		2007		2012		2007		2012		2007		2012		2007	2012	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	
S1																			
T1	18.86	24.73	30.64	22.67	0	0	0	0	0.35	0.4	0	0	0	0	0	0.8	0.9	16.58	35.27
T2	20.33	15.42	29.25	24.28	0	0	0	0	0.1	0.17	3.5	5.7	0	0	0	0	0	0	0
T3	8.61	18.53	32.25	27.79	0	0	0	0	0.86	0.61	0.18	0.36	0	0	0	0	0	0	0
T4	17.49	18.64	39.17	32.85	0	0	0	0	0.51	0.61	0.13	0.17	0	0	0	4.83	13.33	0	0
T5	15.08	14.3	32.32	29.13	0	0	0	0	0.74	0.84	0.61	0.86	0	0	0	1.61	3.01	0	0
S2																			
T1	13.38	22.36	36.27	40.36	0	0	0	0	0.86	1.89	0.59	1.09	3.97	12.57	0	0	0	20.59	36.08
T2	8.63	8.18	49.52	32.04	4.73	14.95	0	0	0.11	0.31	0.37	0.44	0	0	0	0	0	0	0
T3	24.93	18.66	42.08	32.46	0	0	0	0	0.2	0.41	0.67	0.96	0	0	0	0	0	0	0
T4	33.55	28.41	22.76	22.05	0	0	0	0	0	0	0.81	1.22	0	0	0	8.5	14.21	0	0
T5	11.51	14.11	24.83	23.02	0	0	0	0	0.7	0.89	0.85	0.95	0.36	0.15	0	0	0	0	0
S3																			
T1	35.78	23.77	0.53	0.39	0	0	5.33	16	0.06	0.16	0.37	0.75	0	0	0	0	0	21.1	25.59
T2	7.58	8.16	11.77	17.03	0	0	0	0	0	0	0.43	0.57	0	0	0	0	0	0	0
T3	21.05	17.49	25.54	36.45	0	0	0	0	0.06	0.11	0.31	0.34	0	0	0	0	0	0	0
T4	47.31	27.74	18.53	17.56	0	0	0	0	0.18	0.25	0.44	0.53	0	0	0	0	0	0	0
T5	18.61	25.03	12.68	14.75	0	0	7.97	25.21	0.03	0.07	0.39	0.45	0	0	0	0	0	0	0

tests). As in 1975, *Pavona clavus* and *Porites lobata* demonstrated the highest overall live cover, but *Pavona gigantea* and *Pavona varians* also contributed prominently with 7.9 and 5.8 %, respectively (Fig. 5).

#### Radiocarbon dating

Radiocarbon dating of 14 poritid samples from the Wellington Reef ranged from 305 ( $\pm 30$ ) yr to a maximum age of 690 ( $\pm 30$ ) yr (Table 3). Four of six samples collected at the summits of stacks yielded modern dates as did one sample each halfway down (0.85 m) a 1.7-m-high stack, and at the base of a 1.5-m-high stack. Based on the ages of 10 samples, the mean growth rate of frameworks is 0.59 (SD = 0.42) cm yr<sup>-1</sup>, which is evidence for high growth potential. The maximum calculated rate of 2.4 cm yr<sup>-1</sup> was probably due to colony growth and therefore excluded from this estimate. However, the ages of three of the stacks' tops (315–565 yr) also suggest that little net framework accumulation has occurred recently, possibly due to bioerosion after heavy coral mortality. It appears that most of the observed stacks had accumulated during a period roughly 600–300 yr BP and that not much accretion has occurred since.

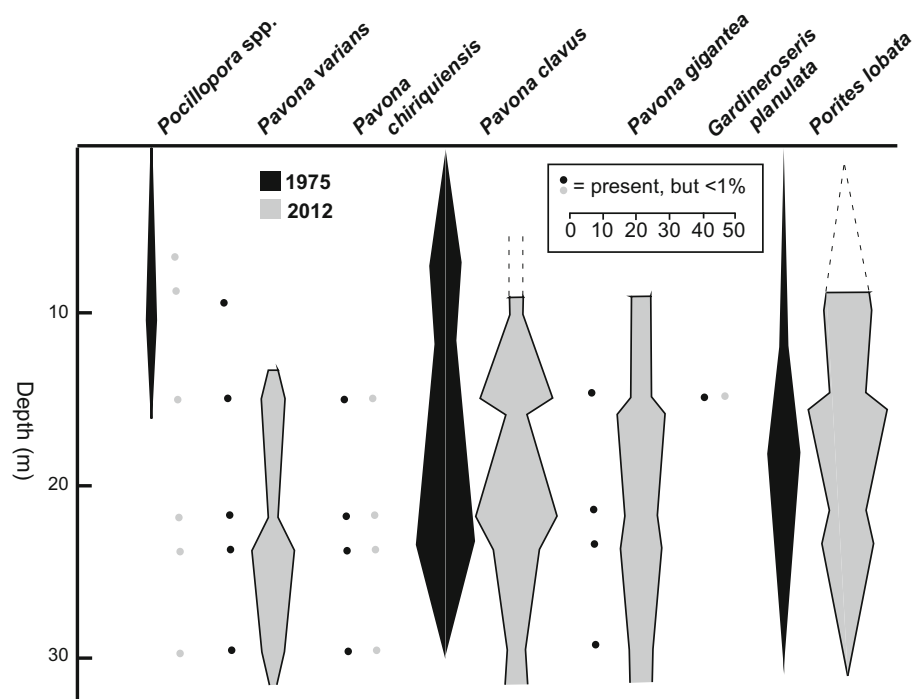
#### *Porites* condition, size, and partial mortality

On the Wellington Reef, mean *Porites lobata* colony sizes, expressed as the heights of the linear skeletal growth axes,

had generally remained the same (Fligner–Killeen test for equal variances,  $p < 0.001$ ; Kruskal–Wallis test for differences among years,  $p > 0.05$ ) from August 2000 to June 2012 (Fig. 6;  $34.6 \pm 36.1$ , SD,  $n = 30$ , in 2000;  $54.5 \pm 39.1$ , SD,  $n = 56$ , 2007;  $36.4 \pm 26.7$ , SD,  $n = 61$  in 2012). Size classes recorded in 2007 had been higher ( $54.5 \pm 39.1$ , SD,  $n = 53$ ). A marked peak in the smallest size class suggests a recruitment pulse or shrinkage of many colonies by partial mortality into the smallest size class, with less mortality in the large size classes. By 2012, this pulse of smaller colonies had graduated into larger size classes, but the high proportion of corals in the smallest size class was maintained, suggesting ongoing sexual reproduction of the population. The two colonies in the 91+ cm size class in 2000 had skeletal growth axes of 150 and 160 cm. In 2007, seven colonies were sampled in this largest size class, and two of them had growth axes of 170 and 200 cm. In 2012, the largest measured colony was 120 cm.

All but three colonies sampled in 2000 contained dead patches, indicative of a high incidence of partial mortality (Fig. 6). Only three colonies in 2007 showed signs of partial mortality. Contrasting the relative ages of these scars, in 2000 78.1 % of colonies exhibited OD patches, and in 2007, no OD patches were observed. The three colonies exhibiting partial mortality (ND) in 2007 represented only 5.7 % of the sample. In 2012, the situation was again similar to that observed in 2000, when most colonies across all size classes exhibited some signs of previous tissue necrosis.

**Fig. 5** Live coral cover over a 30 m depth gradient at Shark Bay (Wenman), from 1975 and 2012 surveys. Dots denote species presence at <1 % cover

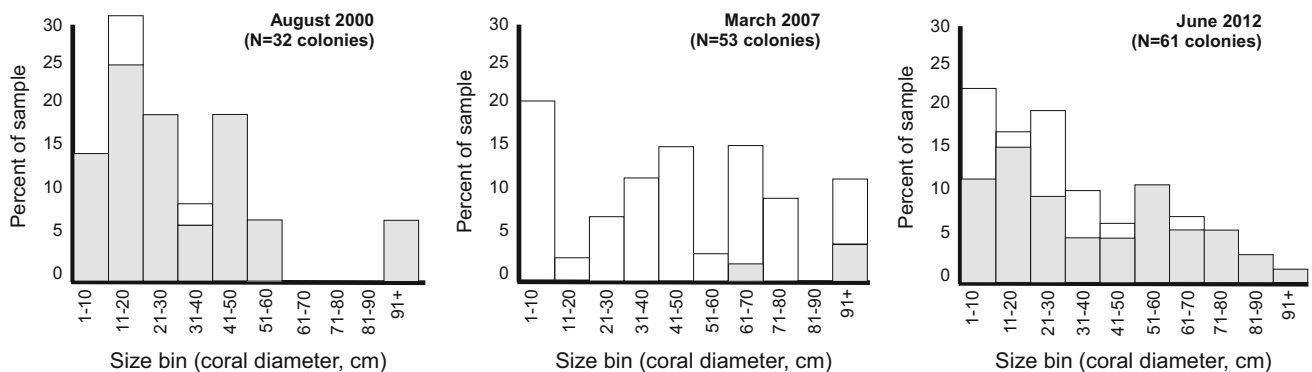




**Table 3** Ages and growth rates of *Porites* stacks at Wellington Reef, Darwin Island

Stack level	Distance down stack (m)	F Modern	Fm Error	Age (yr)	Error (yr)	Growth rate (mm yr <sup>-1</sup> )	Accretion (m Kyr <sup>-1</sup> )
Top	0	0.9336	0.00310	550	25	24	24
Middle	0.6	0.9306	0.00270	575	25	12	12
Bottom	1.2	0.9249	0.00340	625	30		
Top	0	1.076	0.0041	>Modern		3.1	3.1
Middle	0.9	0.9624	0.0037	305	30	3.9	3.9
Bottom	1.8	0.93550	0.00270	535	25		
Top	0	1.0327	0.0039	>Modern		2.2	2.2
Middle	1.2	0.9321	0.00290	565	25	10.4	10.4
Bottom	2.5	0.9174	0.0033	690	30		
Top	0	1.0638	0.0049	>Modern			
Bottom	1.5	1.0653	0.00310	>Modern			
Top	0	1.0409	0.0043	>Modern		2.3	2.3
Middle	1.15	0.93830	0.00290	510	25	7.4	7.4
Bottom	2.3	0.9202	0.0035	665	30		
Top	0	0.932	0.0039	565	35	1.5	1.5
Middle	0.85	1.0377	0.005	>Modern			
Bottom	1.7	0.9291	0.0043	590	35		
Top	0	0.96140	0.00300	315	25	12	12
Middle	1.8	0.9527	0.0037	390	30	4.4	4.4
Bottom	0.9	0.92830	0.00340	595	30		

Growth rate was calculated as distance down stack divided by the age difference over the interval measured of the same distance down stack



**Fig. 6** Size distributions of the linear skeletal growth axes of *Porites lobata* in 2000 (18 August), 2007, and 2012, Wellington Reef. Gray bars denote colonies with dead patches

*Eucidaris*, inter-island abundances, and erosion potential

Estimates of echinoid abundances varied widely across the Galápagos. *E. galapagensis* was ubiquitous, present at all surveyed sites since the mid-1970s (Table 4). It was significantly more abundant in the central/southern (C/S) islands, with an overall mean density of  $18.6 \pm 17.7 \text{ ind m}^{-2}$ , than in the northern islands with a mean density of  $0.9 \pm 0.5 \text{ ind m}^{-2}$

(Mann–Whitney  $U$  test,  $p < 0.0005$ ). Punta Pitt was the only southern island site with a mean density ( $0.3 \text{ ind m}^{-2}$ ) below that of the northern islands. The poritid reef at Bartolomé also demonstrated relatively low *Eucidaris* densities, with a mean value of  $1.4 \text{ ind m}^{-2}$ . *D. mexicanum* was less common, but more frequently encountered in the northern than C/S islands. Other echinoid species *Lytechinus semituberculatus*, *Tripneustes depressus*, and *Centrostephanus coronatus* were more commonly encountered in the C/S islands.

**Table 4** Summary of long-term abundance surveys of echinoids across the Galápagos Islands

Survey site	Period	Habitat	Depth (m)	Species	Mean density no m <sup>-2</sup> (range)	No surveys
Darwin Is						
Wellington Reef	1992–2012	<i>Porites</i> reef, intact	12–20	EG	1.3 (1.2–1.5)	3
				DM	0.1 (0.03–0.2)	
Wenman Is						
Shark Bay	2002–2012	<i>Porites/Pavona</i> community, intact	6–40	EG	0.6 (0.3–1.0)	4
				DM	2.2 (0.7–3.7)	
Pinta Is	1975–2002	<i>Pocillopora</i> patch reef, degraded	2–3	EG	24.5 (14.6–34.4)	2
Bartolomé Is	1975–2009	<i>Porites</i> reef, degraded	2–4	EG	1.4 (1.3–2.1)	3
Santa Cruz Is						
Pta. Estrada	1985–2002	<i>Pavona</i> community, degraded	3–6	EG	10.3 (2.8–21.2)	6
Sante Fe Is						
NE anchorage	1988–2003	<i>Pocillopora</i> patch reef, degraded	1–3	EG	13.0 (0–26.0)	5
				LS	12.2 (4.6–24.8)	
				TD	2.2 (1.6–2.9)	
San Cristóbal Is						
Pta. Bassa	1975–2009	<i>Pocillopora</i> patch reef, degraded	2–3	EG	18.7 (17.2–32.0)	3
				LS	9.4 (4.0–19.1)	
Pta. Pitt	1975–2009	<i>Pocillopora</i> patch reef, degraded	1–3	EG	0.3 (0.2–0.5)	3
Floreana Is						
Devil's Crown	1975–2009	<i>Pocillopora</i> patch reef, degraded	1–3	EG	15.7 (3.9–33.4)	16
				LS	0.9 (0.3–2.4)	
				TD	1.2 (0.1–2.4)	
Champion Is	1985–2009	<i>Pavona</i> patch reef, degraded	6–10	EG	43.4 (18.0–77.0)	7
				CC	0.2 (0–1)	
Española Is						
Xarifa Is	1975–2009	<i>Pocillopora</i> patch reef, degraded	2–4	EG	3.4 (2.0–4.3)	3

EG = *Eucidaris galapagensis*; DM = *Diadema mexicanum*; LS = *Lytechinus semituberculatus*; TD = *Tripneustes depressus*; CC = *Centrostephanus coronatus*

In communities of massive colonies, such as species of *Porites* and *Pavona*, *Eucidaris* abundances may be greatly underestimated due to the echinoid's cryptic sheltering behavior. Sampling of all surfaces of *Porites lobata* and *Pavona clavus* at Devil's Crown, Floreana, revealed numerous individuals sheltering underneath and in the eroded cavities of these massive species. The proportion of cryptic echinoids in 12 colonies sampled ranged from 13.3 to 76.3 % of total urchin counts. Overall, 50.6 % of all individuals occurred cryptically (Table 5). While some were juveniles or young adults (test diameters <3 cm), the majority were comparable in size (4.0–6.0 cm) to those present on exposed surfaces. Expressed as population densities, total *Eucidaris* numbers associated with ~1 m diameter massive corals ranged from 13.1 to 100.0 ind m<sup>-2</sup> (Table 5). A second census conducted at Devil's Crown on October 29, 1987, demonstrated similar results, with 62.7 % of all *Eucidaris* counted occurring cryptically.

At three sites in the southern Galápagos, *Eucidaris* mean bioerosion of massive colonies and reef frameworks ranged

from 13.6 cm (*Pavona clavus*) to 25.2 cm (*Porites lobata*) and from 14.6 to 19.5 cm (*Pocillopora* spp.), respectively (Table 6). This erosion resulted in cylindrical pits, often with a single cidaroid at the bottom. Estimated mean annual rates of erosion, ~2–4 cm yr<sup>-1</sup>, were similar regardless of the coral species substrate. A diminution in the rate of bioerosion with time was apparent in *Porites lobata* at Devil's Crown (4.2–1.8 cm yr<sup>-1</sup> over 3 yr) and the NE anchorage at Santa Fe (3.6–2.0 cm yr<sup>-1</sup> over 4 yr).

## Discussion

Wellington Reef at Darwin exhibits a unique structure, consisting of numerous discrete framework stacks of mostly poritid corals. These stacks do not appear to be isolated remnants of a once continuous reef formation. Three lines of evidence support this interpretation: (a) the absence of fractured surfaces on the stacks, (b) the absence of collapsed stacks or erratic framework blocks, and (c) the

**Table 5** Comparison of visual surface and non-visual cryptic counts of *Eucidaris galapagensis* associated with massive coral colonies

Coral Species	Colony diameter (m)	Number <i>Eucidaris</i>		Percent cryptic	No <i>Eucidaris</i> m <sup>-2</sup>	
		Surface	Cryptic		Surface	Surface + cryptic
<i>Porites lobata</i>	0.7	17	20	54.0	42.5	92.5
<i>Porites lobata</i>	0.9	4	10	71.4	10.0	35.0
<i>Porites lobata</i>	1.1	33	35	51.5	33.0	68.0
<i>Porites lobata</i>	1.5	14	5	13.3	18.3	21.1
<i>Porites lobata</i>	1.3	22	12	35.2	16.9	26.1
<i>Porites lobata</i>	0.8	17	7	29.2	34.0	48.0
<i>Porites lobata</i>	0.7	4	8	66.5	6.7	20.0
<i>Porites lobata</i>	1.3	19	25	56.8	14.6	33.8
<i>Porites lobata</i>	0.9	24	36	60.0	40.0	100.0
<i>Porites lobata</i>	1.3	4	13	76.3	3.1	13.1
<i>Pavona clavus</i>	0.9	9	7	43.8	15.0	26.7
<i>Pavona clavus</i>	1.0	21	20	48.8	26.2	51.2

Surface areas for m<sup>2</sup> conversions calculated from colony diameters

**Table 6** *Eucidaris* erosion rates of massive colonies and pocilloporid frameworks listed chronologically for each survey site

Location	Date	Species	No colonies <sup>a</sup> (n)	Mean depth in carbonate (cm) (SD), range	Mean rate <sup>b</sup> (cm yr <sup>-1</sup> )
Floreana Is					
Devil's Crown	18/4/1989	PL	3 (13)	25.2 (7.2), 15–38	4.2
Cormorant Bay	19/4/1989	PL	3 (15)	18.7 (9.5), 9–35	3.1
		PSPP	5 (28)	14.6 (4.5), 9–24	2.4
Devil's Crown	7/3/1991	PL	3 (27)	22.6 (7.1), 11–37	2.8
		PC	2 (16)	13.6 (2.7), 10–20	1.7
	20/3/1992	PL	3 (27)	16.6 (4.8), 10–30	1.8
		PSPP	2 (15)	19.5 (3.4), 15–25	2.2
		PL	2 (18)	17.7 (6.2), 9–30	2.0
Sante Fe Is					
NE anchorage	19/6/1988	PL	10 (30)	18.0 (7.5), 9–43	3.6
	24/4/1989	PL	3 (17)	18.7 (7.5), 9–29	3.1
	20/3/1991	PL	2 (20)	20.8 (5.5), 11–29	2.6
	23/3/1992	PL	3 (22)	17.9 (5.6), 9–29	2.0

PL = *Porites lobata*; PSPP = *Pocillopora elegans*, *Pocillopora damicornis*; PC = *Pavona clavus*

<sup>a</sup> PSPP, pocilloporid frameworks, number of locations measured

<sup>b</sup> Annual rate calculated from 1983, the year of severe coral mortality

absence of *Porites* rubble piles. Much of the loose rubble associated with the reef is composed of worn and coralline algal-encrusted pocilloporid branches. The estimated maximum vertical thickness of the reef, with stack heights of 3–4 m, is within the same range of some *Pavona* and *Porites* reefs in the C/S Galápagos before the 1982–1983 El Niño event (Table 24 in Glynn and Wellington 1983).

Stack growth on Wellington Reef was rapid between ~700 and 300 yr BP and ranged from 0.2 to 1.2 cm yr<sup>-1</sup>.

Core drilling of a poritid fringing reef at Golfo Dulce, Costa Rica, demonstrated most rapid accretion between 1500 and 500 yr BP, equivalent to accumulation rates of 0.50–0.83 mm yr<sup>-1</sup> or 0.50–0.83 m Kyr<sup>-1</sup> (Cortés 1991; Cortés et al. 1994). Near-shore pocilloporid reefs in Panama have also demonstrated rapid, late Holocene accretion rates (1.2–1.7 m Kyr<sup>-1</sup>) from 1500 BP to the present (Toth et al. 2012). All of the low-end growth rates at Wellington Reef, 1.5–4.4 mm yr<sup>-1</sup>, exceeded those of the Costa Rican Reef

by factors of 3–5. It is not known whether this difference is real or largely a reflection of the different methods employed in the growth history analysis (i.e., carbonate material obtained from surface sampling or subsurface drilling). Another explanation might relate to uninterrupted brief periods of accelerated reef frame growth. For example, several pocilloporid framework accumulation rates determined from samples collected 1.0–2.7 m deep in Panamanian Reefs (Glynn and Macintyre 1977) overlapped the rates calculated for Wellington Reef. Even though both poritid reefs are located outside the tropical cyclone disturbance zone, the Costa Rican Reef formed in a near-shore, sheltered environment, whereas the Darwin Reef developed in an oceanic setting on a semi-exposed insular shelf. Among semi-exposed reefs (not subject to breaking waves), the vertical accretion rate of the Costa Rican Reef was at the low end of reef growth. In comparable settings of Indian Ocean, Western Pacific, and Central Pacific regions, Wellington Reef rivaled the fastest accreting reefs thus far reported (Montaggioni 2005).

With the presently increasing coral cover and abundance of small *Porites* colonies surrounding Wellington Reef stacks, the prospects for continued reef building are favorable. Our surface sampling revealed rapid reef accretion over a 400-yr period, which corresponds to favorable conditions evident in late Holocene climatic reconstructions, namely (1) southerly location of the InterTropical Convergence Zone (ITCZ), (2) low El Niño intensity, and (3) moderate El Niño activity and variability (Enfield 1988; Toth et al. 2012). Coral carbonates were present below the sand sediments at the stack bases, but these were not sampled; therefore, the extent and rate of earlier reef accretion are unknown. Under present-day subtropical, non-upwelling conditions in the northern islands, with relatively low  $p\text{CO}_2$  (mean = 408  $\mu\text{atm}$ ) and high  $\text{pH}_T$  (mean = 8.02), reef framework has persisted, which contrasts with the southern islands that have unfavorable conditions for carbonate preservation (Manzello et al. 2014).

Aside from incipient and patchy framework development at Wenman, i.e., 3.0- to 3.8-m-high poritid stacks at 15–16 m depth, this formation is best regarded as a coral community. Two factors have probably disfavored framework development at Shark Bay, namely (a) the narrow steep shelf (45–65° descending slope) and (b) frequent rock falls that interfere with coral growth, particularly between the low intertidal zone and 10 m depth (Glynn and Wellington 1983). Nonetheless, like Wellington Reef, high coral cover is expected to continue adding to the growth of this community. Overall, high coral cover at Wenman is indicative of recent favorable conditions supporting different species' populations.

The high incidence of dead patches on *Porites lobata* colonies at Darwin in 2012 was likely initiated by cold

water stress and bleaching accompanying the 2007 La Niña. Most of the *Porites lobata* colonies with dead patches in August 2000 could have experienced partial mortality during the island-wide El Niño bleaching in 1997–1998 (Glynn et al. 2001; Podestá and Glynn 2001). Only five colonies (9.4 %) revealed dead patches in March 2007, presumably from tissue regrowth and recovery since the 1998 island-wide bleaching event. A sudden drop in temperature on two occasions in March and April 2007, from 24–28 to 14–18 °C over a few days, caused extensive bleaching of *Porites lobata* (Banks et al. 2009). Symptoms of coral illness were most common in *Porites lobata* in the northern Galápagos in 2007, with discoloration and thinning of tissues, one of the most frequent signs (Vera and Banks 2009). It is probable that the high frequency of dead patches observed in 2012 was a result of thermal shock caused by a rapid transition from moderate El Niño to strong La Niña conditions in early 2007. Thermal shock, notably from elevated temperatures, is known to increase the vulnerability of corals to disease (Lesser et al. 2007; Rosenberg and Kushmaro 2011). Coral tissues are usually lost from diseased surfaces, creating dead patches. Such thermal disturbances have a yet unknown effect on long-term coral calcification and reef accretion in the northern Galápagos.

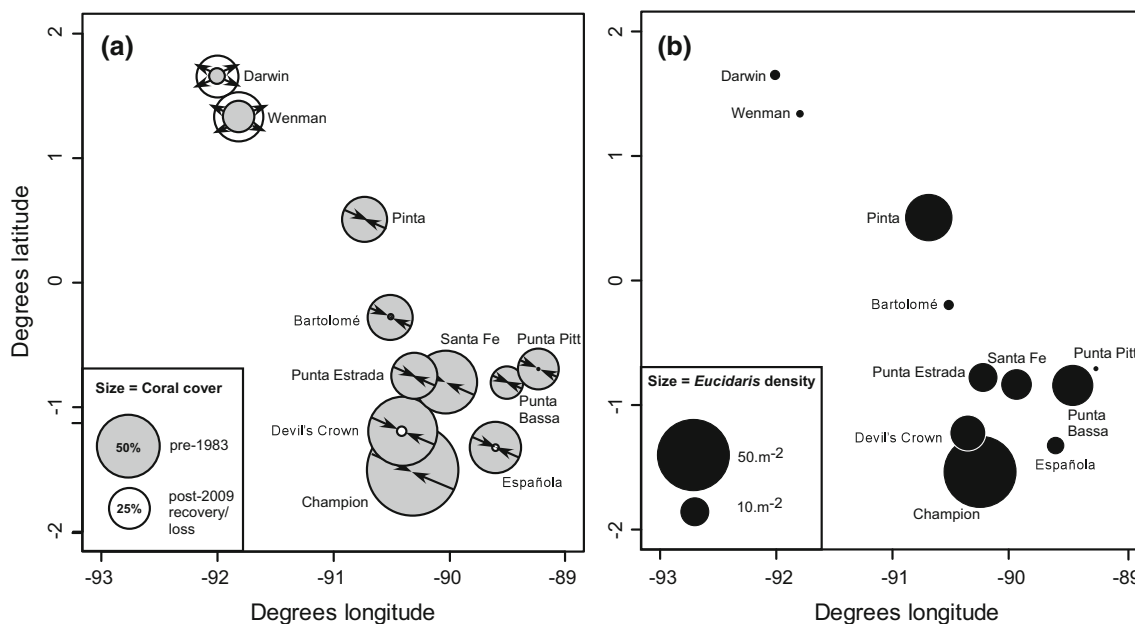
Since the beginning of quantitative surveys in the mid-1970s (1975–1976), *E. galapagensis* has been notably more abundant in the C/S Galápagos than at the northernmost islands of Darwin and Wenman (Glynn and Wellington 1983; Glynn 1994). This pattern, observed in this study and by others (e.g., Edgar et al. 2002), has continued into the twentieth century. At least two factors in the C/S islands seem responsible: (a) a diminution of fish and lobster predators of echinoids due to overfishing (Ruttenberg 2001; Sonnenholzner et al. 2009; Edgar et al. 2010, 2011) and (b) high abundance of trophic resources (benthic algae) in response to upwelling and elevated nutrients (Feldman 1986; Chavez and Brusca 1991). Seven of the nine monitored sites in the C/S islands have demonstrated significant losses of live coral cover coincident with high abundances of *E. galapagensis* and intense bioerosion. Coral cover declined to near zero on the Bartolomé poritid reef with much of the pre-disturbance framework still intact. *Eucidaris* densities have remained low (mean = 1.4 ind  $\text{m}^{-2}$ ) at this site, as at Wellington Reef, but no recovery has occurred (as of 2009). The low fecundity of *Porites lobata* in the Galápagos (Glynn et al. 1994) and the depletion of reproductive source populations after 1983 (Glynn 1994) were likely responsible for this lack of recovery. Low abundances of *Eucidaris* (mean = 0.3 ind  $\text{m}^{-2}$ ) were observed during three surveys at the Punta Pitt pocilloporid reef. However, this patch reef was rapidly degraded within 10 yr after the 1982–1983 bleaching/mortality event. The relatively few *Eucidaris*

observed on this dead reef were grazing on, and eroding, the algal-encrusted pocilloporid frameworks. Large numbers of *Eucidaris* were present in the general area, but not on the reef during the surveys. We suspect that many echinoids moved from the sampling site beforehand, thus minimizing estimates of their local abundances.

At monitored sites across the Galápagos, Darwin and Wenman were the only localities where coral cover increased after the disturbance associated with the 1982–1983 ENSO (Fig. 7a). While coral cover was also depressed in the northern islands initially, a significant and continuous upward trend of recovery nonetheless occurred. The most important coral cover in the southern islands, with slight regeneration, was observed at Devil's Crown, off Floreana. An aggregation of *Porites* colonies still persists there (Paul 2012), but the pre-1982–1983 *Pocillopora* reef has been completely degraded. *Pocillopora* sexual recruits appear sporadically at the former reef site only to dieback during periods of ENSO thermal shock (Feingold and Glynn 2014). Low recovery of coral cover, and absence of any coral frameworks in the C/S islands, is mirrored by high densities of *E. galapagensis* and severe bioerosion (Fig. 7b). The intensive grazing and skeletal excavation by *E. galapagensis* on dead coral frameworks resulted in their disintegration and disappearance at eight of nine monitored sites. This protracted erosive effect likely interfered with coral recruitment as well (Glynn 1990).

In addition, two physical conditions characteristic of the C/S islands—upwelling promoting high nutrient concentrations, and low carbonate saturation state—have been demonstrated to depress coral calcification and internal cementation (Manzello et al. 2008; Manzello 2010). As a consequence, coral skeletal density is low in the C/S islands, which increases the fragility and integrity of coral skeletons. This in turn would exacerbate the degradation of coral structures due to bioerosion.

Information is now available on timelines and processes involved in the recovery of reefs on remote, oceanic islands. Isolation of oceanic reefs from major human influences vis-à-vis pollution and over-fishing is likely an important factor in coral community resiliency. This potential advantage, however, needs to be balanced against coral larval supply and recruitment to distant disturbed communities. Although coral mortality was not quantified in the northern Galápagos following the 1982–1983 El Niño bleaching event, it was probably in the same range of 80–98 % reported for 14 C/S island coral communities (Robinson 1985; Glynn et al. 1988). By 1992, much of the Wellington Reef framework was still intact, in spite of obvious erosion by *D. mexicanum*, with numerous *Porites* recruits present on dead corals (Glynn 1994). Overall, live coral cover in 2009 was 21 %, and this increased to 38 % by 2012, 29 yr after the initial disturbance (Glynn et al. 2009). Recovery of live coral cover on Cocos Island reefs, ~ 700 km NE of



**Fig. 7 a** Coral cover trajectories on two northern and nine central/southern Galápagos islands following the 1982/1983 El Niño bleaching/mortality event. Outward and inward pointing arrows denote increasing and decreasing coral cover, respectively.

**b** Corresponding *E. galapagensis* mean densities, from multiple quantitative surveys, 1975–2012. Geographic position of Champion Island offset in 'a' and 'b'

Darwin, reached 23 % after 20 yr (Guzman and Cortés 2007). Bioerosion by *D. mexicanum* was intense on some reefs, causing the degradation of reef frameworks (Guzman and Cortés 1992; Macintyre et al. 1992). However, *Diadema* abundances decreased significantly after 1987, from 11–17 to 0.1–1.4 ind m<sup>-2</sup> by 2002, resulting in a greatly diminished impact on regenerating resident colonies. Five new coral records during the recovery of Cocos Reefs, all central Pacific species, prompted Guzman and Cortés (2007) to suggest that long-distance dispersal via the North Equatorial Counter Current may contribute toward reef recovery. Nonetheless, the chief reef-building species present before the mortality event were the same as those undergoing recovery. Even more rapid reef recovery was reported at the remote Scott Reef complex in the Indian Ocean off of Western Australia (Gilmour et al. 2013). Overall, coral cover increased from 9 %, down from ~50 % pre-1998 bleaching, to 44 % in just 12 yr. This notable recovery was due to post-disturbance growth of local remnant corals, after increasing in size and reproductive capacity, thus elevating their contribution to sexual recruitment and community growth. These examples underline the pivotal role of surviving autochthonous corals and their importance in reproduction and sexual recruitment.

In summary, persistent grazing of substrates by large populations of *Eucidaris* interferes with coral settlement, survivorship, and community recovery. Furthermore, carbonate reef structures are subject to intense bioerosion, thus eliminating suitable firm substrates for coral recolonization. If fishing pressure of macro-invertebrate predators of sea urchins were reduced, this could result in lower population abundances of *Eucidaris* and contribute toward the re-establishment of decimated coral communities and reefs in the central and southern Galápagos Islands. Patterns revealed in this study emphasize the importance of temporal dynamics and spatial variability in reef carbonate budgets, resilience, and persistence (Perry et al. 2008).

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