RESEARCH ARTICLES

RAPID RECOVERY OF A CORAL REEF AT DARWIN ISLAND, GALAPAGOS ISLANDS

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SUMMARY

Surveys at Darwin Island in 2006 and 2007 have demonstrated that this northernmost Galapagos Islands coral reef has recovered significantly since the 1982–3 El Niño event. When first surveyed in 1975, this structural reef exhibited actively accreting frameworks of pocilloporid and poritid corals. The coral suffered severe mortality in 1983, resulting in the near total loss of pocilloporids and extensive partial mortality of poritid corals. Large sections of the reef had not recovered by 1992 and dead frameworks were subject to bio-erosion, although small numbers of sexual recruits of pocilloporid corals and numerous recruits plus regenerating patches of *Porites lobata* were present in some areas. An increase in live coral cover and recruitment was apparent through 2000 and 2002. Recent sampling at three sites along the reef has demonstrated mean (± 1 SD) live coral cover of 21.9 ± 1.7 % with *P. lobata* as the predominant species. *Pocillopora* spp. were present, but not so abundant as in earlier surveys. In spite of moderate erosion by echinoid and fish grazers, much of the original coral framework remained intact, providing a substrate for coral regeneration and recruitment. Recovery can be attributed to the original reef structure remaining intact, asexual regrowth of surviving tissues and sexual recruitment of poritid corals from surviving source populations.

RESÚMEN

Recuperación rápida de un arrecife de coral en la Isla Darwin, Islas Galápagos. Investigaciones en la Isla Darwin en 2006 y 2007 han demostrado que en esta isla, la más al norte del archipiélago de las Galápagos, los arrecifes de coral se han recuperado de una manera significativa desde el advenimiento del fenómeno de El Niño de 1982–3. Cuando se realizaron las primeras observaciones en 1975, este arrecife mostraba crecimiento activo de corales, especialmente de las familias Pocilloporidae y Poritidae. En 1983 los corales sufrieron mortandad severa lo que resultó en la pérdida casi absoluta de pocilopóridos y una mortandad generalizada de los porítidos. Grandes porciones del arrecife aún no se habían recuperado en 1992, y las estructuras coralinas muertas habían sido afectadas por la bio-erosión, aun que un número pequeño de reclutas sexuales de corales pocilopóridos y numerosos reclutas y parches regenerativos de *Porites lobata* se avistaron en algunas áreas. La recuperación continuó en marcha tanto en el 2000 como en el 2002. Recientemente, muestreos llevados a cabo en tres localidades a lo largo del arrecife han demostrado un promedio (± 1 DE) de cobertura de coral vivo de 21,9 ± 1,7 % y una dominancia de *P. lobata. Pocillopora* spp. estaban presentes, pero no tan abundantes como en muestreos anteriores. A pesar de erosión ocasionados por erizos y peces, la mayoría de la estructura coralina permaneció intacta y esto ha proporcionado un sustrato para la regeneración del coral y el reclutamiento. La recuperación se puede atribuir a que la estructura coralina ha permanecido intacta, el crecimiento asexual del tejido sobreviviente, y el reclutamiento sexual de los corales porítidos provenientes de las poblaciones sobrevivientes de coral.

INTRODUCTION

The resistance and resilience of member species influence the recovery of biotic communities affected by disturbances. Community resistance, the ability to avoid displacement by alternate species assemblages, is greater if member species can withstand perturbations. Resilience, the ability of a community to recover from a

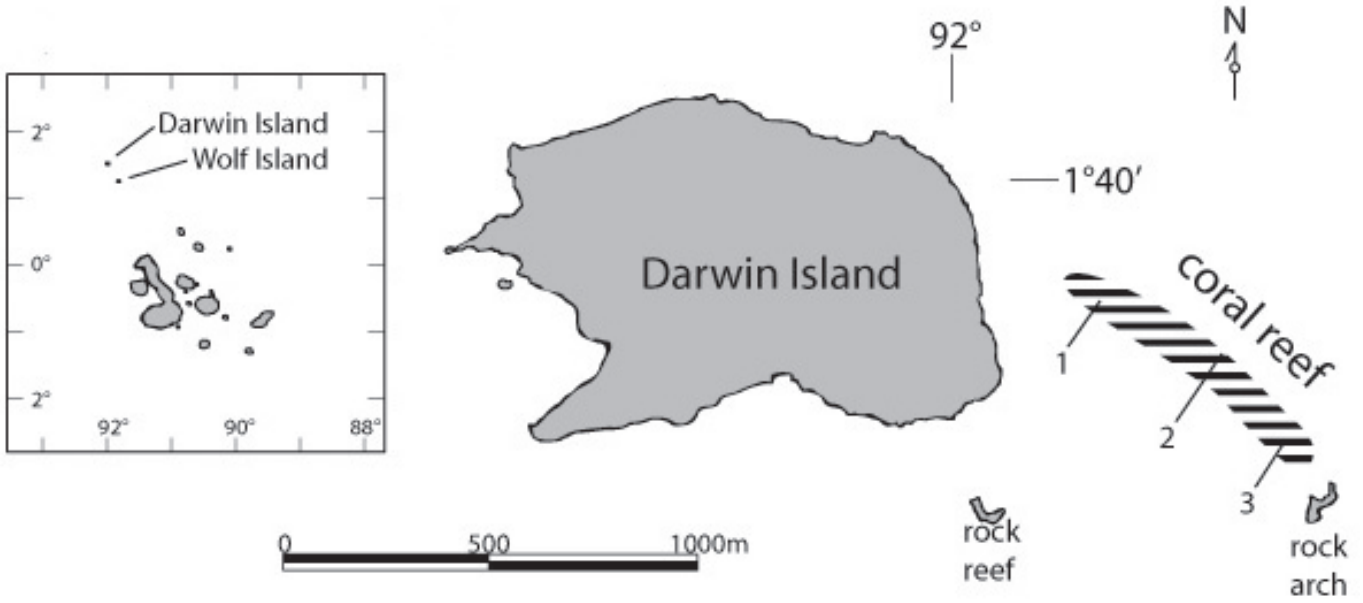

Figure 1. Location of Darwin and Wolf Islands in the Galapagos Archipelago, and approximate position of the Darwin Island coral reef and sampling sites.

disturbance, is enhanced by species that can quickly re-establish populations to pre-disturbance levels. In E Pacific reef-building coral communities, certain species can survive periods of elevated temperature anomalies (*e.g. Porites lobata* and *Pavona clavus*), and others colonize communities through sexual recruitment after such disturbances (*e.g. Pocillopora* spp. and *Psammocora stellata*). Related to resilience is the availability of surviving source populations that can supply propagules capable of recruiting to degraded communities. This study centers on these aspects of community dynamics, focusing on a Darwin Island coral reef that was seriously degraded by sea warming episodes during the past two decades.

Like many coral reef ecosystems worldwide (*e.g.* Hoegh-Guldberg 1999, Gardener *et al.* 2003, Bellwood *et al.* 2004, Wilkinson 2004), the coral reefs of the Galapagos Islands have suffered severe declines since the early 1980s (Robinson 1985, Glynn 1994, Wellington & Glynn 2007). The 1982–3 El Niño event was accompanied by high sea temperatures that caused extensive coral bleaching (loss of symbiotic zooxanthella photobionts and their photosynthetic pigments) and mortality throughout the archipelago (Robinson 1985, Glynn 1990). The objectives of this study are to describe the location, geomorphology and coral species composition of the Darwin Island coral reef, and to assess its recovery over the 25 years following the 1982–3 El Niño disturbance.

MATERIALS AND METHODS

Darwin or Culpepper Island is centered at 1°39′20′′N, 92° 0′30′′W. A structural coral reef is located on the insular shelf at 8–18 m depth, with its long axis trending NW–SE between the island's east shore and Darwin's rock arch (Fig. 1). The reef was surveyed in 1975, but only briefly described (Glynn & Wellington, 1983). Subsequent surveys were conducted on 26 Mar 1992, 18 Aug 2000, 18 May 2002, and 21–23 May 2006. More recently, the extent of the reef and quantitative sampling of the epibenthic cover along its length were initiated on 6 and 7 Mar 2007. The location of the reef and sampling sites were determined from a Quickbird satellite image with 2.4 m multispectral resolution, taken on 25 Feb 2005, and hand-held differential Global Positioning System (GPS) fixes (*c.* 5 m precision) at various positions along the reef. From this image, we obtained the reef's general outline.

Dead coral framework heights were measured in 1992, 2000 and 2007 to determine the extent of erosion following the 1982–3 El Niño disturbance. This was accomplished by two divers, one holding a weighted tape measure at the summit of a formation and the other sighting and signaling the horizontal elevation from the adjacent sand plain. Framework formations adjacent to the reef floor or with skeletal shafts leading to the reef base were selected for measurement. Sampling was biased toward the higher framework elevations.

Live coral cover was quantified in 2007 from 10 photographs of 0.25 m^2 quadrats laid at predetermined random locations along each of 15, 10 m length transects. Three sets of 5 transects, each running perpendicular to the long axis of the reef and separated by 5 m, were completed at sites 1, 2 and 3 (Fig. 1).

During the reef surveys in 2000 and 2007, the height and diameter of *Porites lobata* Dana colonies first encountered at sampling sites 1 (2000) and 1–3 (2007) (Fig. 1) were measured, and percentage estimates of the live and dead surface areas of each colony were recorded. The dead areas were further classified as "old dead" (OD) and

"new dead" (ND), where OD were defined as dead patches serving as substrates for large barnacles, azooxanthellate corals and/or thick crusts of coralline algae, with skeleton highly eroded, and ND were dead patches overgrown by filamentous algae and/or thin crusts of coralline algae, with skeleton not highly eroded and fine structure of calices still visible.

During the 2006 survey, tissues from *Porites lobata* and its endosymbiotic algae (*Symbiodinium* spp.) were collected from 15 colonies at Darwin and Wolf (Wenman) Islands (Fig. 1). Samples were collected from the upper surfaces of colonies and fixed in 95 % ethanol. DNA was extracted using an organic protocol (Rowan & Powers 1991, Baker *et al*. 1997), and the Internal Transcribed Spacer region 2 (ITS-2) was amplified using primers designed by LaJeunesse & Trench (2000). Distinct amplicons within the reaction products of each sample were then separated using Denaturing Gradient Gel Electrophoresis (DGGE) on a 35–75 % gradient gel according to the general methods described by LaJeunesse (2002). Individual bands were excised from DGGE gels, the DNA was extracted and reamplified, and the PCR products were directly sequenced using the BigDye terminator method and an automated DNA sequencer (Applied Biosystems 3730xl). Edited sequences were then identified by BLAST searches in GenBank (http://www.ncbi.nlm.nih.gov/BLAST/).

RESULTS

The estimated length of Darwin reef is *c.* 700 m, with the westernmost terminus located *c.* 225 m off Darwin Island's east shore at *c.* 10 m depth (Fig. 1). In its eastward extension, the reef bends gradually toward the southeast and ends *c.* 100 m from Darwin's rock arch at 18 m depth. At its center, the reef is *c.* 90 m wide. Calcareous sand flanks both the shallow shelf and deeper (N–NE) sides of the reef. A large fraction of the coral rubble on the reef floor and in off-reef sediments consists of pocilloporid branches commonly ranging from 10–20 cm in length.

Eleven zooxanthellate coral species were observed on the reef: *Porites lobata*, *Pavona clavus* Dana, *Pavona gigantea* Verrill, *Pavona chiriquiensis* Glynn, Maté & Stemann, *Pavona varians* Verrill, *Pocillopora elegans* Dana, *Pocillopora damicornis* (Linnaeus), *Pocillopora eydouxi* Milne-Edwards & Haime, *Pocillopora meandrina* Dana, *Pocillopora* sp., and *Psammocora stellata* (Verrill). *Tubastrea coccinea* Lesson, an azooxanthellate species, was also present and common on exposed reef substrates. Crustose coralline algae, turf algae and leathery macroalgal crusts covered most of the reef substrate not occupied by scleractinian corals. Other noticeable epifaunal species nearly always present in Galapagos coral reef communities included the echinoid bio-eroders *Diadema mexicanum* A. Agassiz and *Eucidaris galapagensis* Döderlein, and the acorn barnacle *Megabalanus peninsularis* (Pilsbry), a competitor for space on dead and live coral skeletons. The Guineafowl Puffer *Arothron meleagris* (Bloch & Schneider) was a common obligate corallivore and

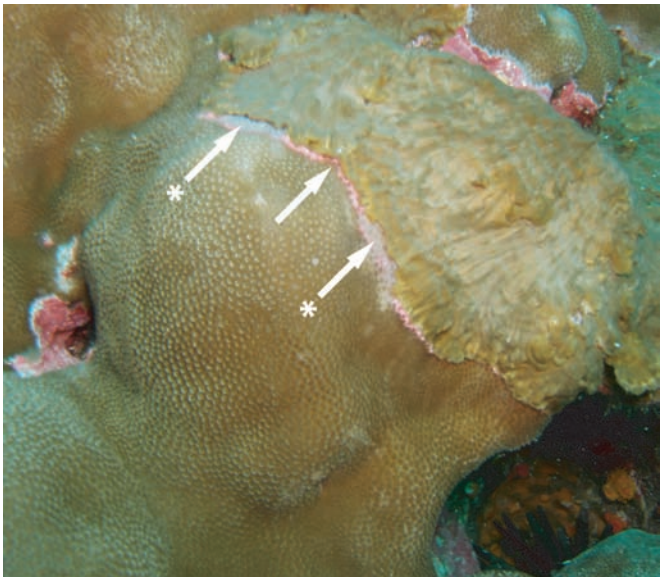

Figure 2. *Peyssonnelia boergesenii* Weber-van Bosse, an encrusting brown alga apparently overgrowing live *Porites lobata* tissues. Arrows point to the coral-algal interface. * = pink margin between coral tissue and alga. Diameter of alga *c.* 20 cm. Darwin reef, 12 m depth, 6 Mar 2007.

Yelloweye Filefish *Cantherhinus dumerilii* (Hollard), another corallivore, was also present. *Acanthaster planci* (Linnaeus) was sometimes observed feeding on coral during our surveys. However, it has been seen only at Darwin Island.

Several interphyletic species interactions were observed. *Peyssonnelia boergesenii* Weber-van Bosse, a brown macroalgal crust, commonly occurred and evidently grew over the living tissues of *Porites lobata* (Fig. 2). The coral skeletons underlying the alga were recently dead and retained their detailed structure, suggesting recent overgrowth by the alga. Pink pustules along the peripheral growing edges and neoplasms were also commonly seen on poritid colonies. *Megabalanus peninsularis* occurred in patches on many of the larger live colonies of *P. lobata* (Fig. 3). The rasping scars of echinoids were prominent, but generally on dead algal-covered substrates and not live corals. The puffer and filefish were both observed biting off pieces (0.5–1.0 cm) of live *P. lobata*.

Many colonies of zooxanthellate coral species exhibited mild to moderate bleaching in deeper and cooler waters on Darwin reef, other sites around Darwin Island and at Wolf Island (about 40 km SE of Darwin Island). The species exhibiting bleaching at 10–15 m were *Porites lobata*, *Pocillopora* spp., *Pavona clavus* and *P. gigantea*. This bleaching was first observed in early March 2007 during a cold shock event of upwelled water following slightly elevated and protracted temperatures from a moderate El Niño up to March. There was a 12ºC decline (28º to 16ºC) at 15 m depth over a six-day period at the end of February, and another cold event of similar magnitude in May (S. Banks pers. comm.).

Mean poritid reef framework structures ranged in height from 1.97 m in 2007 to 3.67 m in 2000 (Table 1). Due

Table 1. Dead *Porites lobata* framework heights in four years on the western sector (near site 1) of Darwin Island coral reef. Measurements are in meters and biased toward the higher elevations encountered in the sampling areas.

Year	N	Range	Mean (SE)
1992	5	1.8–3.4	2.46 (0.32)
2000	3	2.0–5.0	3.67 (0.88)
2006	6	1.0–4.0	2.73 (0.44)
2007	15	1.0–2.7	1.97 (0.12)

to small sample sizes and inconsistent interannual site sampling, it is not possible to test for temporal changes. However, these data indicate that, although the tallest structures seem to have disappeared by 2007, the dead poritid frameworks are largely still intact and have retained much of their relief following two severe El Niño events (1982–3, 1997–8). Pocilloporid coral frameworks, present in 1975, were absent from all surveyed areas. Instead, numerous dead pocilloporid branches were present on the sand bottom among dead standing poritid frameworks and in areas immediately surrounding the reef. The *Pocillopora* spp. colonies observed during surveys from 2000 to 2007 were isolated, not growing in juxtaposition.

Total reef-wide coral cover amounted to 21.1 % in 2007 (Table 2). *Porites lobata* predominated, contributing 19.5 % to the total (Fig. 3). *Pavona clavus*, *Tubastrea coccinea* and *Pocillopora* spp. each contributed < 0.4 % to the total cover. The differences in total coral cover were not significant among transects or sites ($P > 0.05$, F1 = 2.89, F2 = 2.91,

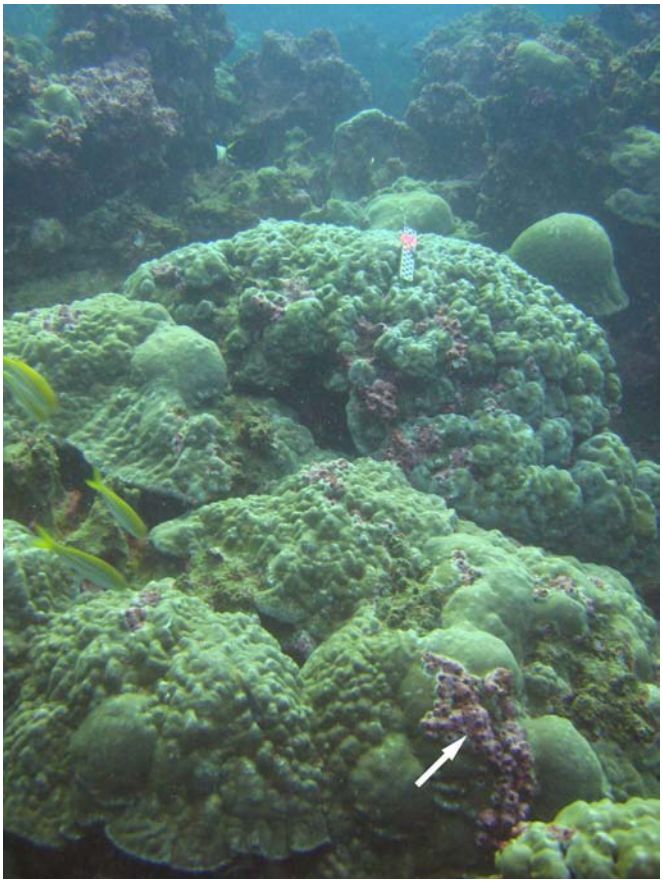

Figure 3. *Porites lobata* colonies that survived the 1982–3 El Niño event. Most colonies are encrusted with patches of the acorn barnacle *Megabalanus peninsularis* (arrow). Scale resting on coral colony in background is 20 cm in length. Darwin reef, 12 m depth, 6 Mar 2007.

Table 2. Live coral cover (% ± 1SD of 0.25 m^2 sample squares) of key species on Darwin Island reef in 2007. S1–3 = sample sites 1–3, Fig. 1; T1–5 = transects 1–5 at each sample site.

		Porites lobata	*Pavona clavus*	*Tubastrea coccinea*	*Pocillopora* spp.	Site mean live cover
S1:	**T1**	18.86 ± 24.73	0	0.35 ± 0.40	0	16.58
	T2	20.33 ± 15.42	0	0.10 ± 0.17	0	
	T3	8.61 ± 18.53	0	0.86 ± 0.61	0	
	T4	17.49 ± 18.64	0	0.51 ± 0.61	0	
	T5	15.08 ± 14.30	0	0.74 ± 0.84	0	
S2:	**T1**	13.38 ± 22.36	0	0.86 ± 1.89	3.97 ± 12.57	20.59
	T2	8.63 ± 8.18	4.73 ± 14.95	0.11 ± 0.31	0	
	T3	24.93 ± 18.66	0	0.20 ± 0.41	0	
	T4	33.55 ± 28.41	0	0	0	
	T5	11.51 ± 14.11	0	0.70 ± 0.89	0.36 ± 1.15	
S3:	**T1**	35.78 ± 23.77	0	0.06 ± 0.16	0	26.14
	T2	7.58 ± 8.16	0	0	0	
	T3	21.05 ± 17.49	0	0.06 ± 0.11	0	
	T4	47.31 ± 27.74	0	0.18 ± 0.25	0	
	T5	18.61 ± 25.03	0	0.03 ± 0.07	0	
					Overall reef mean	**21.10**



Figure 4. Several live *Porites lobata* colonies on eroded colonies killed during the 1982–3 El Niño event. Scale is 20 cm in length. Darwin reef, 12 m depth, 6 Mar 2007.

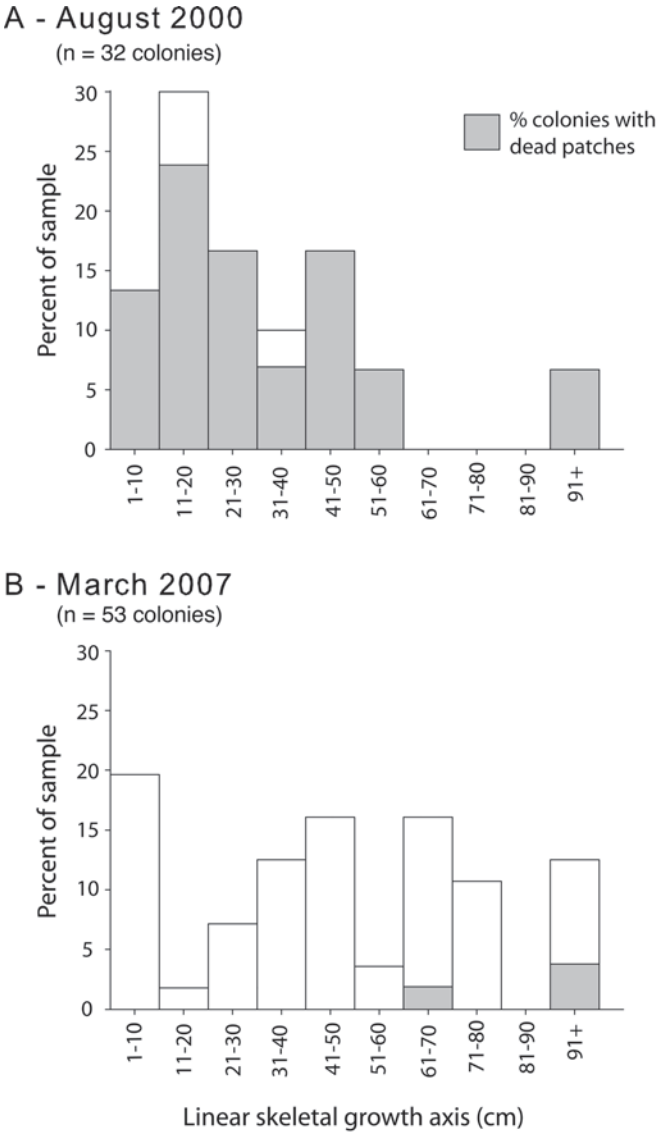

Figure 5. Size-class frequency distributions of the linear skeletal growth axes of *Porites lobata* on Darwin reef in August 2000 and March 2007.

nested ANOVA). The reef framework consisted of large dead massive *P. lobata* colonies with smaller live colonies affixed to the upper surfaces of the former (Fig. 4). Although it was not possible to identify the species of *Pocillopora* in the phototransects, the majority of the colonies sampled were *P. elegans* and *P. eydouxi*. Pocilloporid species and all other non-poritid zooxanthellate species were more abundant or only observed along the deeper (15–18 m) reef edge.

Mean *Porites lobata* colony sizes, expressed as the heights of the linear skeletal growth axes, demonstrated significant increases ($P = 0.0023$, Mann Whitney U test) from August 2000 to March 2007 (Fig. 5). The incremental increase in the sample colony sizes over the nearly 7-year period was 19.9 cm (54.5 ± 39.1, SD, n = 53, 2007; 34.6 ± 36.1, SD, n = 32, 2000). The size-class distributions in both years contained relatively high proportions of young colonies. Relatively higher proportions of colonies were 35 cm or larger in 2007 compared with the sampled population in 2000. 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.

All but three colonies sampled in 2000 contained dead patches, indicative of a high incidence of partial mortality (Fig. 5, Table 3), while only three colonies in 2007 showed signs of partial mortality. Contrasting the relative ages of these scars, in 2000 78.1 % of colonies exhibited old dead patches, and in 2007 no old dead patches were sampled. The three colonies exhibiting partial mortality (new dead) in 2007 represented only 5.7 % of the sample.

Five unique symbiont band profiles were detected by DGGE analysis within the 15 *Porites lobata* colonies sampled (Fig. 6); three of the profiles contained previously unreported sequences. All *Symbiodinium* identified were members of clade C, with sequences exactly or nearly matching type C15 (at most, three base pairs different). The C15 type and a novel band profile (C15-1) were most common, detected from five and six of the colonies sampled, respectively.

Table 3. Numbers of *Porites lobata* colonies on Darwin reef with old (OD) and new (ND) dead patches sampled in March 2000 and 2007. Because some colonies contained both old and new dead surfaces, the total number of scars may exceed the number of sampled colonies.

		Colony condition		Relative age	
Year	n colonies	No scars	Scars present	OD	ND
2000	32	3	29	25	12
2007	53	50	3	0	3

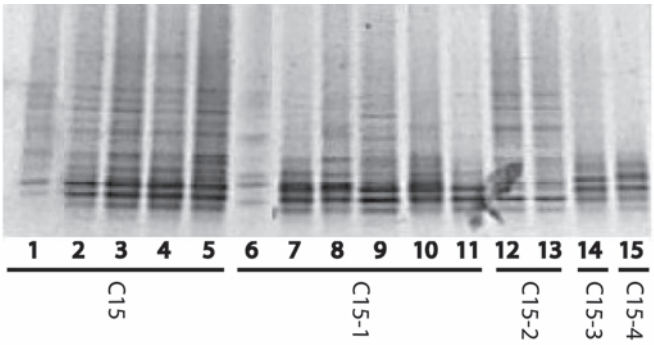

Figure 6. DGGE analysis of the ITS-2 region (285 base pairs) of *Symbiodinium* sampled from *Porites lobata* colonies (numbered 1–15) from Darwin and Wolf Islands in 2006. Sampled colonies containing symbionts with identical band profiles are each grouped by a horizontal bar, with the *Symbiodinium* type (C15 to C15-4) identified from that band profile shown below the bar. Collection depths for each *Symbiodinium* type (C15 to C15-4) were 7–15, 12–20, 11–13, 11 and 6 m, respectively.

DISCUSSION

All coral reefs in the central and southern Galapagos Islands that experienced high mortality (*c.* 95 %) during the 1982–3 El Niño event were further degraded by several years of intense bio-erosion (Glynn 1988, Reaka-Kudla *et al.* 1996). Reef frameworks were converted to rubble and sand by internal and external bio-eroders. Among the latter, *Eucidaris galapagensis* has been the most destructive. It erodes about ten times the mass of coral and coralline algae as *Diadema mexicanum*, and its population density was commonly 15–30 m^{-2} on dead coral substrata (Glynn *et al.* 1988). *Diadema* was present only at low densities (< 1 m^{-2}) on dead reef structures. In contrast, the northern islands of Darwin and Wolf support relatively few *Eucidaris* and higher abundances of *Diadema*. For example, the highest mean abundances were: *Diadema* (sampled at night) 3.5 m^{-2} and *Eucidaris* (day sampling) 0.54 m^{-2} (Bustamante *et al.* 2002). It is highly likely that the intact coral frameworks at Darwin Island owe their existence to the relatively low levels of bio-erosion. In the long term, the persistence and growth of coral reefs depend on the presence of former structures that can support coral regeneration and recruitment. Colgan (1990) attributed the modest reef buildups in the Galapagos Islands to intermittent El Niño-induced bleaching and death, and then the bio-erosion and loss of limestone substrates.

Pocilloporid reef frame bio-erosion was also high in Panamá following the 1982–3 El Niño event (Glynn 1990, Eakin 1996). This was caused chiefly by *Diadema mexicanum*, which dramatically increased in abundance after 1984, from <10 m^{-2} pre-event to 50–90 m^{-2} through the mid-1990s. Since 2000, *Diadema* abundances have declined to <10 m^{-2} (Eakin 2001), and live *Pocillopora* spp. patches are now present on remnant framework substrata. Coral mortality in Panamá was significantly lower following the 1997–8 bleaching event, 13 % compared with 75 % in 1982–3 (Glynn et al. 2001). Reef recovery, *i.e.* an increase in live coral and initiation of framework growth, is presently occurring on many reefs in Panamá (Glynn & Fong 2006).

High abundances of *Tubastrea coccinea* were commonplace on open (upper) reef substrates. This azooxanthellate species is generally cryptic in the E Pacific, occurring on the undersides of massive corals and other stable structures. Even though it contributed little (0.32 %) to the total live cover, hundreds of colonies were present in the photoquadrats. Colonies are typically small, *c.* 3–8 cm in diameter (2–12 polyps). It is possible that the large numbers of *T. coccinea* settled and grew in response to the available habitat space resulting from the high coral mortality in the early 1980s.

In 1975, the west end of Darwin reef, the only reef sector surveyed at that time, consisted of large sections of live pocilloporid frameworks. These were about 1 m in vertical thickness and covered massive pavonid and poritid colonies. No pocilloporid buildups, live or dead, were observed at any of the survey sites in 2006 or 2007. Pocilloporid rubble, however, was scattered over the bottom across the entire reef. Since the chief frame-building species in March 2007 was *Porites lobata*, the reef is presently diminished in terms of its structural diversity. Several sites sampled in the Galapagos Islands during the 1997–8 El Niño event showed *P. lobata* to have lower mortality rates than pocilloporid corals (Glynn *et al.* 2001). Thus, the prominence of *P. lobata* is likely due to its resistance to elevated temperatures and subsequent renewed growth of surviving tissues (Glynn & Fong 2006). In addition, the numerous young colonies (2–10 cm, skeletal growth axis) are indicative of successful recruitment, an attribute of species resilience.

Photophysiological differences between *Symbiodinium* spp. within coral species and individuals contribute to variations in bleaching response (Warner *et al.* 1996, Iglesias-Prieto *et al.* 2004), and this has been linked to symbiont genetic diversity (*e.g.* Berkelmans & Van Oppen 2006, Warner *et al.* 2006). Corals that can flexibly host different symbiont types may therefore be better able to cope with environmental perturbations. Although *Symbiodinium* clades C and D have previously been detected within *Porites lobata* (Baker 1999), only clade C symbionts were detected within the individuals sampled in 2006 from the northern Galapagos Islands. Furthermore, ITS-2 sequence differences between the symbiont band profiles from these colonies are minimal and likely to represent intraspecific variation. Ongoing analysis of additional coral colonies will be useful in understanding *Symbiodinium* spp. distributions within the Galapagos Islands, and how these distributions may influence the persistence and current dominance of *P. lobata* in this region, despite recurrent El Niño bleaching events.

Corallivore feeding scars, caused primarily by the pufferfish *Arothron meleagris* and the filefish *Cantherhinus dumerilli*, were commonplace on *Porites* colonies. The bite scars were usually concentrated along colony ridges or

protuberances. The scars ranged from recently bitten to various stages of regeneration. In no instance was a colony entirely consumed. The gastropod *Coralliophila violacea* (Kiener) was also observed grazing on some *Porites* colonies. A single *Acanthaster planci*, a seastar corallivore, has been observed feeding on corals at Darwin Island, but in areas away from the coral reef. *Acanthaster* is rare in the Galapagos region (Glynn 2003). Therefore, corallivore concentration on remnant corals surviving El Niño disturbances or small recruits does not seem to have been an important factor in the recovery of the Darwin Island coral reef. The recovery of coral reefs at Cocos Island, Costa Rica also has not been thwarted by corallivores (Guzman and Cortés 2007).

Based on an analysis of skeletal density bands by X-radiography, the mean elongation rate of *Porites lobata* over a 12-year period at Marchena Island, in the thermally highest sector (Harris's zone 3, see Banks 2002) of the mid-Galapagos Islands region, was 8.9 (± 1.0 SE) mm yr^{-1} (Glynn 1994). Applying this mean growth rate to the modal size class sampled in 2000, colonies in this cohort likely recruited from 22 to 12 years previously, *i.e.* from 1978 to 1988. The largest size class sampled in 2007 consisted of smaller colonies that probably recruited from 11 to *c.* 1 year ago. Since seawater temperatures are generally higher at the northernmost islands of Wolf and Darwin compared to Marchena, with likely commensurately higher growth rates, the skeletal extension rates used here may overestimate the age of coral recruits. Nonetheless, these size classes and the relatively abundant larger and older size classes in both years suggest that the recruitment of *P. lobata* has continued over the past 25 years and longer in spite of severe El Niño events.

The high abundance of colonies with dead patches in 2000 (93.8 %) compared with 2007 (5.7 %) is indicative of the regeneration and healing of surviving coral tissues over this 7-year period. In addition, the proportion of colonies in 2000 with old dead (78.1 %) compared with new dead (37.5 %) scars implies that coral mortality was greater during the 1982–3 than the 1997–8 El Niño event. Indeed, Glynn *et al.* (2001) documented higher mortality rates for *Porites lobata* during the earlier event.

Darwin reef is one of the few coral reefs in the Galapagos that has not lost its structural integrity through bioerosion (Glynn 2003). Its persistence and stability have allowed the regeneration of surviving coral patches and the settlement of coral recruits following recent El Niño disturbances. The coral reefs at Cocos Island (Costa Rica), located on the Cocos Ridge about 440 km NE of Darwin Island, have experienced a similar degree of recovery as Darwin Island (Guzman & Cortés, 2007). Overall coral cover of five reefs at Cocos Island was 23 % in 2002, compared with 21 % at Darwin Island in 2007. The dominant species in both regions was *Porites lobata*. In an earlier report on the recovery potential of reefs at Cocos Island, Guzmán & Cortés (1992) predicted that full recovery (including attainment of the original, pre-1983 reef framework thickness) would require centuries. The present state of reefs at Cocos and Darwin Islands indicates that significant recovery is in progress, including the initiation of coral framework construction.

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