NOTE

El Niño-associated disturbance to coral reefs and post disturbance mortality by *Acanthaster planci*

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ABSTRACT: Coral reefs in the tropical eastern Pacific region experienced catastrophic coral mortality during the severe 1982/1983 El Niño event. *Pocillopora* spp., the dominant scleractinian reef-building corals, were most seriously affected, resulting in large tracts (0.1 to 1 ha) of dead reef surface in Costa Rica, Panamá, Colombia, and the Galápagos Islands, Ecuador. A sea star *Acanthaster planci* is now entering centrally-located reef areas in Panamá corals and is feeding on large, massive corals formerly surrounded and protected by live *Pocillopora* corals and their symbiotic crustacean guards. This note outlines the effects of El Niño-related differential coral mortality and subsequent mortality resulting from the elimination of a protective biotic barrier The ages of corals killed during the initial physical disturbance, and later by predation, allow an estimate of the period of uninterrupted reef growth, i.e. the minimum number of years since an earlier, major El Niño event: about 190 yr on the basis of present evidence.

Warm tropical waters have traditionally been regarded as beneficial to coral reef development and growth (Dana 1843, Wells 1957, Kinsman 1964, Rosen 1971, Stehli & Wells 1971). Occasionally, however, intense natural warming of reef waters has resulted in localized, reef-building coral mortality (Shinn 1966, Jaap 1979, Yamazato 1981). The course of such events has typically involved a stress to the coral and its symbiotic algae (zooxanthellae) with the loss of zooxanthellae ('bleaching'), and subsequent recovery or death of the host coral colony. The El Niño event of 1982/83, regarded as the strongest this century (Halpern 1983, Kerr 1983), accompanied widespread coral mortality in the equatorial eastern Pacific region in 1983 (Glynn 1983a, Lessios et al. 1983, Glynn 1984a). The abnormally high sea surface temperatures (mean values 30 to 31 °C), their duration (5 to 6 mo, Glynn 1984a), and depth of isotherm penetration (nearly 100 m deeper in some areas than in previous years, Rebert et al. 1983), were probably in large part responsible for the disturbance.

Coral mortality was generally highest among species exhibiting the most rapid skeletal growth, e.g.

Pocillopora spp. and *Millepora* spp. (hydrocorals). Several surviving coral species, previously protected from coral-eating sea stars because of their location on the reef, were exposed to predation following the El Niño-associated catastrophe. These mortality events were observed on coral reefs located off the Pacific coast of Panamá in the Gulf of Chiriquí, at Uva Island (7°48′ 46″ N; 81°45′ 35″ W), Contreras Islands, and at an
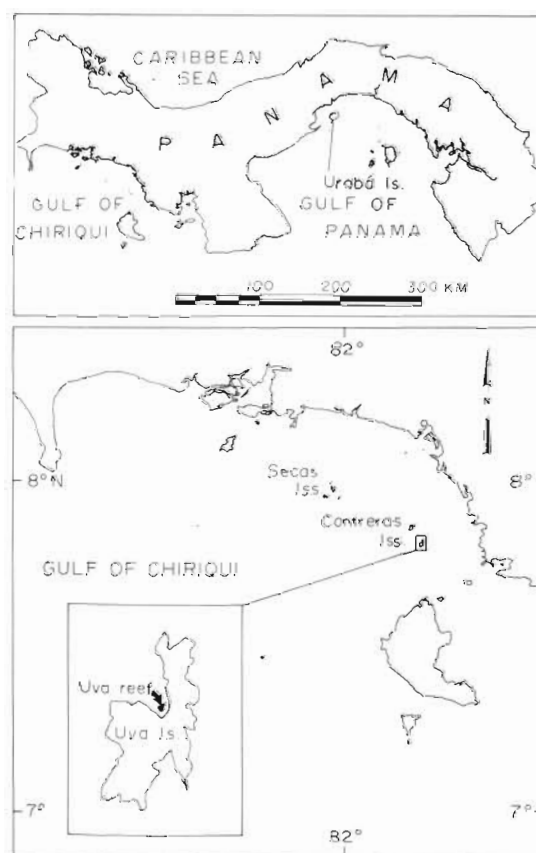

Fig. 1. Study areas showing locations of Uva Island and Secas Islands, Gulf of Chiriquí, and Urabá Island, Gulf of Panamá

un-named island (7° 51' 18" N; 82° 00' 45° '' W), Secas Islands (Fig. 1).

Branching pocilloporid corals are the chief reef-builders in the eastern Pacific (Glynn et al. 1972, Porter 1972a, b, 1974, Glynn 1976, Glynn & Wellington 1983). *Pocillopora damicornis* (Linnaeus) is usually the most abundant species with *P. elegans* Dana also present on most reefs. Less than 10 other coral species of massive, platy and nodular growth forms contribute to eastern Pacific reef frameworks. In areas where the sea star corallivore *Acanthaster planci* (Linnaeus) is present, these nonpocilloporid species are often less abundant and are generally smaller in size compared with corals in reef areas without this corallivore (Glynn et al. 1982, Glynn & Wellington 1983, Glynn et al. 1983). Nonpocilloporid corals present on the deep (8 to 10 m) edges of reefs are frequently attacked and eaten by *A. planci* (Glynn 1973, 1976). *A. planci* has demonstrated a consistent feeding preference for several of the nonpocilloporid coral species in Panamá (Glynn 1976,
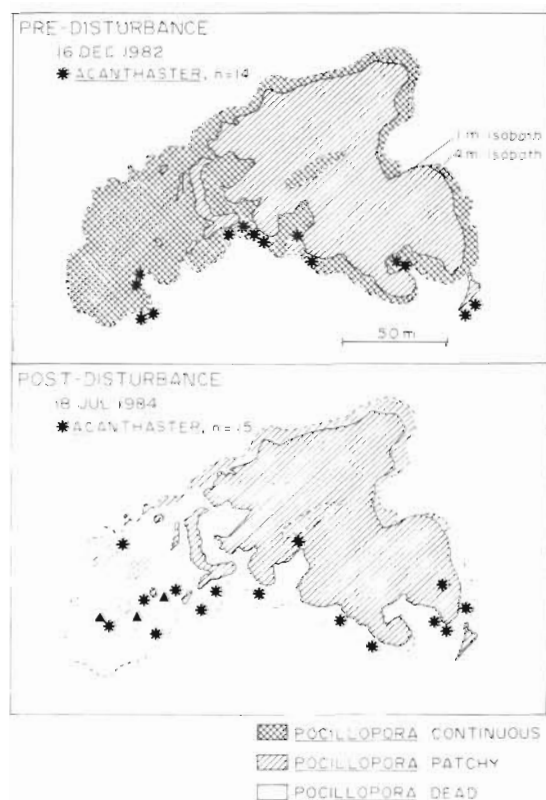

Fig. 2. Plan views of Uva Island patch reef showing the distribution and relative abundance of live *Pocillopora* spp. corals before and after the 1983 coral mortality event. Continuous stands of *Pocillopora*, from 3 to 8 m depth, were killed; 1 and 4 m isobaths indicated relative to the MLWS tidal datum. Abundances and locations of *Acanthaster planci* also shown. The 3 triangles in the northern reef zone show the locations of large massive corals attacked by *A. planci* after March 1983. Major features of reef maps according to survey conducted in 1972 (Glynn 1973)

Glynn et al. 1983). The principal nonpocilloporid corals are *Gardineroseris planulata* (Dana), *Pavona clavus* Dana, *Pavona gigantea* Verrill, and *Pavona varians* Verrill. Since 1970 all large colonies of *G. planulata* (n = 74 colonies with maximum diameters $\geq$ 0.25 m) have been attacked by *A. planci* in these deep reef habitats, resulting in total to near-total colony death. All of these colonies have undergone erosion and collapse or have served as substrata for other coral settlement (e.g. *Pavona varians* and *Pocillopora elegans*), but have not shown any significant regeneration.

On parts of reefs where *Pocillopora* spp. are abundant, especially where these corals form encircling, continuous, live tracts, nonpocilloporid species are often present and sometimes reach large sizes. The occurrence of nonpocilloporid corals among dense stands of *Pocillopora* spp. seems to be due to a refuge effect, wherein the latter prevent the entry of foraging *Acanthaster planci* into centrally-located (core) reef areas. *A. planci* does not move over continuous stands of *Pocillopora* spp. because of the coral's nematocyst defenses (Barnes et al. 1970) and possession of crustacean guards (*Trapezia* and *Alpheus*) which attack and repel sea stars (Glynn 1976, 1983b). The catastrophic coral mortality accompanying the 1982/83 El Niño in the eastern Pacific resulted in the death of large tracts of *Pocillopora* spp. and their crustacean guard symbionts. This nullified the protective effect of *Pocillopora* spp., thus allowing *A. planci* access to reef areas with favored coral prey. Compare the pre- and post-disturbance patterns of *Pocillopora* abundance and the corresponding location of foraging *A. planci* in Fig. 2. The numbers of crustacean guards per coral colony and the frequency of aggressive responses toward *A. planci* declined significantly during the period of coral 'bleaching', morbidity and death (Fig. 3). The decline in guard density and defensive behavior was probably due to the deteriorating condition of host corals, and not a direct result of the general sea warming. Coral mucus and entrapped detritus represent the normal food source for these obligate crustacean symbionts (Knudsen 1967, Patton 1974, 1976, Castro 1976, Glynn 1983c), and mucus release declined significantly in the affected corals (Fig. 3A). Lipid levels also declined in stressed host corals and symbiotic crabs, suggesting that the crustacean guards were affected by food deprivation (Glynn et al. 1985).

One group of 22 colonies of the massive coral *Gardineroseris planulata*, previously (before April 1983) encircled by live *Pocillopora* spp., had shown no evidence of predation by *Acanthaster planci* since 1972, when it was first observed. By 30 October 1983, about 6 mo after the near-total death (up to 95 %) of surrounding *Pocillopora* spp. (Glynn 1984a), *A. planci* had entered the reef core and was feeding on the largest of
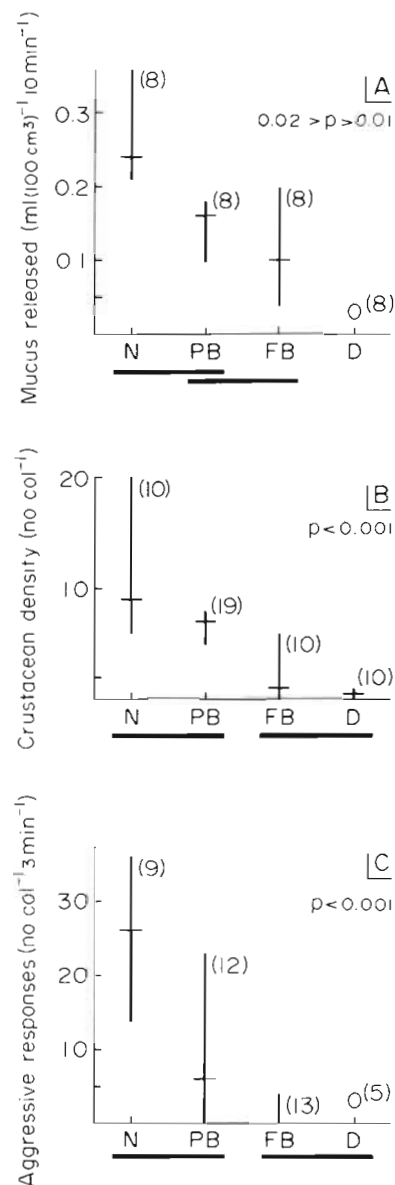
Fig. 3. Decline in mucus release (A), crustacean guard density (B), and crustacean defense (C) in host colonies of the coral *Pocillopora damicornis* during the 1983 mortality event in Panamá. Crustacean guards included 4 species of the xanthid crab *Trapezia*, and the alpheid shrimp *Alpheus lottini*. Coral condition: N, normal-appearing with full brown pigmentation; PB, partially 'bleached'; FB, fully 'bleached'; D, dead. Median values, 0.95 confidence limits of medians, and number of colonies sampled (in parentheses) shown for each condition. Kruskal-Wallis significance levels indicated in each plot; horizontal lines along abscissas join statistically equal median values (multiple comparison procedure, α = 0.15). Mucus release was determined by 'milking' (inverting and shaking gently) corals, then collecting the crude mucus and determining its volume (Glynn 1983b, c); Urabá Island, Gulf of Panamá (8° 47′ 03″ N; 79° 32′ 22″ W), 14 June 1983; Md (median) colony diameter = 9 cm (8 to 10 cm, 0.95 conf. lim. of Md). Crustacean densities are total number of crab (*Trapezia* spp.) and shrimp (*Alpheus lottini* Guerin) guards found in individual colonies that were bagged *in situ*, dislodged and processed in the laboratory (Glynn 1976); Uva and Secas study reefs, 23 to 24 June 1983; Md colony diameter = 14 cm (14 to 15 cm). Simulated feeding attacks with live *Acanthaster planci* (disc diameters = 13 to 16 cm) were used to quantify the aggressive defensive responses of coral crab and shrimp guards (Glynn 1983b); Uva study reef, 27 to 28 April 1983; Md colony diameter = 27 cm (25 to 29 cm). Colony size was similar (p > 0.05, Kruskal-Wallis test) among treatments (coral condition) for each of the 3 tests

the colonies in this group. Approximately 0.20 m² of the surface of the largest colony (10 % of the total live tissues) had been killed by October, and 0.40 m² (20 %) by 18 July 1984. Up to 95 % of the live surfaces of other colonies in this group had also been killed by *A. planci* by mid July 1984. The feeding scars caused by *A. planci* were readily distinguishable from the upper summits of colonies that were discolored and damaged during the El Niño event. From October 1983 to July 1984, *A. planci* was feeding on other groups of *G. planulata* and on platy and encrusting colonies of *Pavona varians* in other reef core areas that were also formerly surrounded and protected by live *Pocillopora* spp. (Fig. 4).

Cores up to 254 cm in length were drilled from *Gardineroseris planulata*, cut along the growth axis to

4 mm thickness, and X-rayed for density band and growth rate analyses (Buddemeier 1978, Macintyre 1978). Individual corallites could be traced intact along the growth axes. Since most colonies of *G. planulata* were nearly perfectly symmetrical (hemispherical mounds) and exhibited continuous skeletal growth, it is unlikely that they have undergone significant colony death, as observed after 1983, since their recruitment onto the reef. Thus, the oldest colony, whose 2 cores (232 and 254 cm length) showed no major discontinuities, should provide an estimate of the time that this group of nonpocilloporid corals has been encircled by a living, protective belt of *Pocillopora* spp.

This means of prey protection via a biotic refugium assumes that *Acanthaster planci* has been an important

Fig. 4. *Acanthaster planci* feeding on colony of *Gardineroseris planulata* formerly (before March 1983) encircled and protected by dense stands of live *Pocillopora* spp. coral (22 Jun 1984, 5 m depth). Arrows 1 and 2 point respectively to a dead patch of *G. planulata* killed by *A. planci* (left, same sea star feeding on another patch on same colony, maximum diameter arm tip-arm tip ≈ 30 cm), and dead *Pocillopora* over which sea stars have moved to reach reef core areas

predator on the Uva reef during this period. The first documented record of *A. planci* in the eastern Pacific is from La Paz, Mexico, reported in 1869 (Verrill 1869, Madsen 1955). Relatively stable population sizes of *A. planci*, observed in Panamá since 1971 (Glynn 1982, 1984b), are also assumed. The largest, and presumably oldest colony was 254 cm in height, had a mean annual growth rate of 1.3 cm, and grew continuously for about 192 yr (Table 1). While some skeletal growth irregularities were found, major growth hiatuses and corroded surfaces due to partial mortality or waxing and waning growth were not observed as in some corals (Hughes & Jackson 1980, Jackson 1983). A large colony of *Pavona gigantea* grew continuously for 122 yr, and the thickest vertical exposures of the pocilloporid reef frame indicated uninterrupted growth for 41 yr (Uva reef) and 73 yr (Secas reef) Longer mean growth periods are indicated for pocilloporid frameworks that were excavated and aged by C-14 dating (130 to 140 yr, Table 1), but these are net accumulation rates, usually involving different coral colonies, crustose coralline algae, etc., and represent combined growth and erosional events.

Another line of evidence from the core drilling indicates that *Acanthaster planci* did inhabit the Uva reef before the largest colony of *Gardineroseris planulata* was recruited onto the reef. After the oldest section of the colony was cored and retrieved, the drill hole was re-entered and underlying sediments were obtained from 302 cm depth, i.e. at 48 cm beneath the original colony attachment site. These sediments were examined for *A. planci* skeletal remains, after Frankel's (1977) method, and one skeletal element was found in 1.25 kg (dry weight) of sample analysed. This result indicates that *A. planci* was present in the area 200 yr ago. More extensive sampling (Glynn unpubl.) at 3 sites on the deep reef edge revealed the presence of *A. planci* skeletal elements in 9 of 16 samples collected from the surface to 150 cm deep in the carbonate sediments. Although the ages of these skeletal elements are presently unknown, it seems probable that *A. planci* has been present on the Uva reef during at least the last 200 yr

The high growth rate of *Pocillopora* spp. compared with massive corals (about 3 times as fast) is probably one of the chief reasons why the former are predomi-

Table 1. Estimated periods of maximum uninterrupted coral colony growth and net coral reef frame growth, Gulf of Chiriquí, Panamá

Sample	Maximum vertical length along growth axis (cm)	Growth rate (cm yr^{-1})	Period of continuous growth (yr)
Gardineroseris planulata, colony, Uva study reef, 30 Oct 1983	254	1.32 (1.2–1.4)[a]	192 (185–204)
Pavona gigantea, colony, Secas Islands (7°57'50"N, 82°01'40"W), 14 Dec 1980	110	0.90 (0.8–1.1)[b]	122 (100–138)
Pocillopora damicornis, exposed reef frame, Uva study reef, 30 Oct 1983	160	3.90 (3.4–4.3)[c]	41 (37–47)
Pocillopora damicornis, exposed reef frame, Secas study reef, 31 Oct 1983	285	3.90 (3.4–4.3)[c]	73 (66–84)
Pocillopora damicornis, excavated reef frame, Secas study reef, 25 Mar 1971	270	2.08 (1.3–6.0)[d]	130 (45–215)
Pocillopora damicornis, excavated reef frame, Secas study reef, 23 Sep 1972	200	1.43 (1.0–2.5)[d]	140 (80–200)

[a] Range of mean growth rates from 3 transects (colony surface to 50 cm deep in colony) from same colony
[b] Range of median colony growth (N = 15 colonies, Glynn et al. 1983)
[c] 0.95 confidence limits of mean coral growth (Glynn 1977, Glynn & Macintyre 1977)
[d] Mean ±1 SD, based on C-14 date (Glynn 1977, Glynn & Macintyre 1977)

nant on eastern Pacific reefs. Nonpocilloporid species escape attacks from *Acanthaster planci* among dense stands of *Pocillopora* spp., but this kind of protection is usually only temporary. Sooner or later, perhaps on a time scale of 100 or few 100s of years, *Pocillopora* spp. will overtop and dominate reef surfaces. Severe El Niño disturbances that differentially kill branching corals would tend to slow down the potential domination by *Pocillopora*. On a shorter time-scale (10s of years), other conditions may also impede the growth of *Pocillopora*, e.g. disturbances differentially affecting but not necessarily killing ramose corals (Bak & Luckhurst 1980, Highsmith 1982, Hughes & Jackson 1985) or minor El Niño warming spells that limit growth while still leaving protective coral stands intact. If the death of branching corals is too extensive, however, this protective barrier would be eliminated, thus allowing the entry of sea star corallivores into massive coral refugia.

I have also observed that massive corals with associated fishes, sharks, and spiny lobsters that use the eroded coral bases for shelter often have a bare zone (halo) of coarse sediment surrounding the colony. The persistence of this zone, probably in large part aided by the associated animals seeking shelter, would prevent the establishment, encroachment and overgrowth of branching corals immediately adjacent to massive colonies.

In summary, present indirect evidence suggests that coral and reef growth have proceeded continuously in Panamá during the past 190 yr. A severe El Niño, of the magnitude of the 1982/83 disturbance, has probably not visited Panamá over this period.

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