

Predicted disappearance of coral-reef ramparts: a direct result of major ecological disturbances

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Abstract

Two coral cays near La Parguera, Puerto Rico, have large, exposed coral ramparts composed almost entirely of loose pieces of elkhorn coral *Acropora palmata* (88% of horizontal transects, 98% of vertical transects). The total volume of elkhorn coral in the ramparts of the two cays was estimated at 3600 and 12800 m³. The present volume of living elkhorn coral on these two reefs was estimated at 7 and 14 m³ and previous volumes at 11000 and 34900 m³. White-band disease was found on 8.5% of living elkhorn colonies. Lang's boring sponge *Cliona langae* covered 10.8% of the total transect area, overgrowing both dead and living corals. White-band disease and coral-reef bleaching have drastically reduced the populations of elkhorn coral, thus, skeletal coral materials to replenish the plate ramparts are severely reduced, disrupting the process of forming and maintaining these coral reef ramparts. We predict that the next series of major storms striking these prominent cay ramparts will remove them. These disappearances will represent a quick, obvious and permanent consequence of global disturbances. Loss of cay ramparts will modify the environments on and around Atlantic coral reefs. Ramparts may be similarly lost from Indo-Pacific reefs. The lack of any other indisputable definitive indicators of long-term, major disturbances on coral reefs makes the distinct loss of coral-reef ramparts an important physical sign.

Keywords: coral cay, reef rampart, elkhorn coral, marine major ecological disturbances, prediction, white-band disease

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Introduction

The formation of coral cay ramparts is an intricate and interdependent process. Major storms break elkhorn coral, *Acropora palmata* (Lamarck) (Cnidaria: Scleractinia: Acroporidae), thickets from the seaward side of Caribbean coral reefs and pile the material onto the reef flat forming distinctive, exposed plate ramparts. Large-scale ecological disturbances have drastically reduced or removed these thickets from the shallow fore reef. We believe that with almost no elkhorn coral to replenish the plate ramparts, the next series of major storms striking these reefs will wash away the exposed ramparts rather than rebuild them.

Coral cays are small islands on top of coral reefs in which the emergent portions are often composed of loose or cemented coral plates (Figs 1,2) (Hernandez-Avila *et al.* 1977; Flood & Scoffin 1978). The exposed parts of Caribbean cays are composed principally of elkhorn coral which has broken off the reef crest and has been piled onto the reef flat by major storms (Glynn *et al.* 1964; Hernandez-Avila *et al.* 1977). Cay ramparts on outer, high-energy reefs are almost completely elkhorn coral; more protected inner, lower-energy reefs (Figs 1,2) have more sand, vegetation and detritus in addition to the elkhorn rampart. If outer cay ramparts disappear, inner cays will receive more wave energy and may also eventually erode away. Skeletons of elkhorn coral form loose plate ramparts from the surface of the sea up to 4.5 m a.s.l. on cays exposed to high wave energy (Hernandez-Avila *et al.* 1977), protect the cays from wave erosion, and allow

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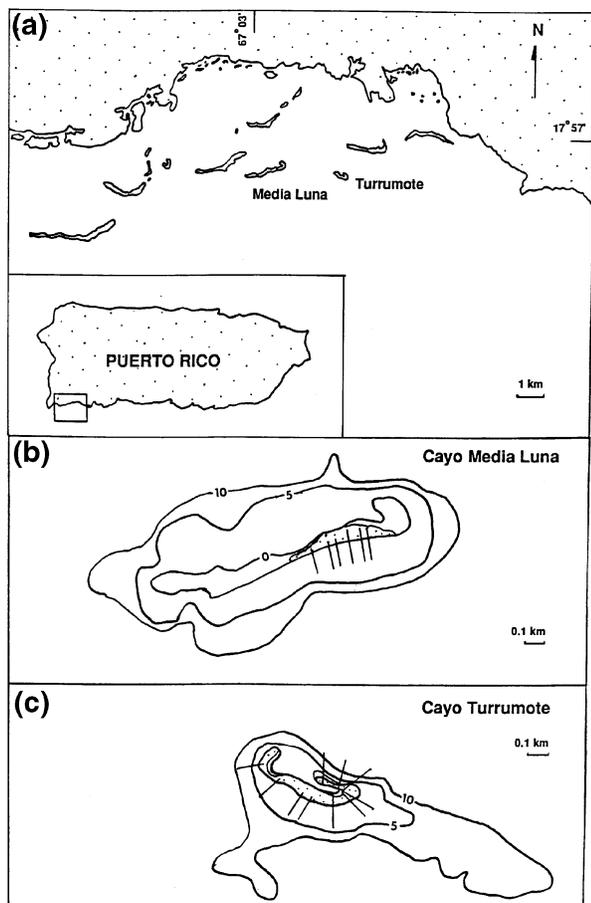


Fig. 1 (a) Reefs of south-western Puerto Rico with the Island of Puerto Rico in insert. Land areas stippled. (b) Cayo Media Luna (21) (c) Cayo Turrumote. Modified from a map by Dr Jack Morelock. Stippled areas = plate rampart, straight lines = transects, contour lines marked on 0, 5 and 10 m depths.

coral rubble and sand to accumulate. These should more appropriately be called 'plate ramparts' in the Caribbean rather than 'boulder' or 'shingle' ramparts. 'Boulder' (any large rock worn and rounded by weather and water) and 'shingle' (coarse round gravel on the seashore) are defined geological terms that do not apply to calcium carbonate materials. Caribbean ramparts are composed almost entirely of plates of elkhorn coral. Their plate form allows these corals to be easily detached from the reef, more easily transported onto the reef flat than those with massive forms, and yet form a cohesive riprap against wave energy. Indo-Pacific and a few low Caribbean ramparts are composed of rubble from branching corals, such as *Porites porites furcata* Lamarck and *Acropora cervicornis* (Lamarck) (Flood & Scoffin 1978). We suggest 'rubble rampart' (from coral rubble) might be the best term for ramparts formed by these coral

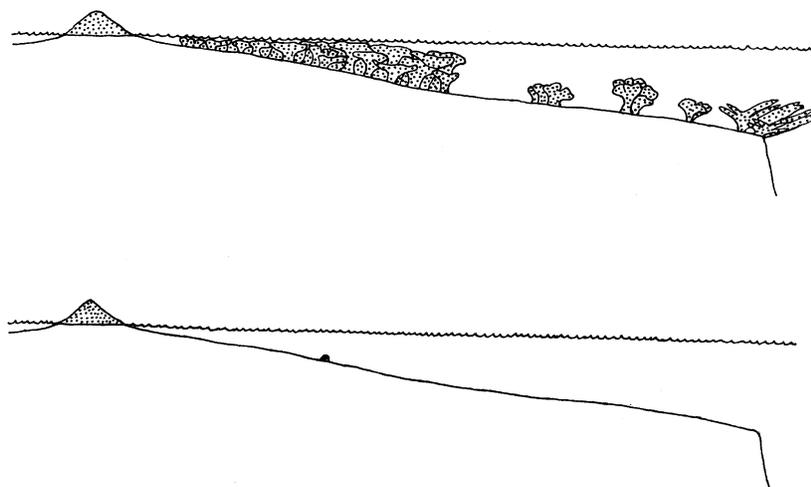
pieces. Accumulations provide further stability by allowing mangroves and other vegetation to become established. Coral reef cays also protect back-reef, lagoon, mangrove and shore environments. Some are used for human habitation.

Elkhorn coral (Fig. 3) once formed dense, high-profile, monospecific stands (= thickets) in the shallow (1–5 m) fore reef zone (Fig. 2) and was abundant throughout the tropical Western Atlantic (Goreau 1959; Colin 1978; van Duyl 1982). Since the late 1970s, this coral has been drastically reduced in abundance by white-band disease (WBD) (Gladfelter 1982; Peters *et al.* 1983; Williams & Bunkley-Williams 1990a; Bunkley-Williams *et al.* 1991), and since 1987, it has also been adversely affected by repeated coral-reef bleaching (CRB) (Williams *et al.* 1987, 1991; Williams & Bunkley-Williams 1990a,b; Bunkley-Williams *et al.* 1991). Epizootics of WBD have raged in elkhorn coral in most Western North Atlantic reefs. Worldwide major CRB events occurred in 1980, 1983, 1987 and 1990 and more recently. We have been attempting to follow CRB and other disturbances since 1987 with the Marine Ecological Disturbance Information Center and an information network of field observers. Elkhorn is one of the fastest growing and regenerating reef-building corals in the Atlantic (Bak 1983). In the past, storm-damaged thickets have regenerated between major storms and thus produced the skeletal coral materials to replenish the cay ramparts during subsequent storms. The elkhorn thicket also absorbed routine wave energy and protected the cays.

We hypothesized that: (i) Caribbean coral reef cay ramparts are composed almost exclusively of elkhorn coral; (ii) extant living elkhorn coral is now so reduced compared with amounts available when the cay ramparts were formed that insufficient material is available to replenish the ramparts; and thus (iii) coral reef cay ramparts will soon disappear throughout the Western North Atlantic.

White-band disease and CRB cause marine major ecological disturbances (MMEDs) (Williams & Bunkley-Williams 1990a; Bunkley-Williams *et al.* 1991). One of the difficulties in evaluating the importance of MMEDs lies in the lack of immediate, easily measurable effects on the environment and humanity (Williams & Bunkley-Williams 1990a; Bunkley-Williams *et al.* 1991). Definite evidence of forces which possibly drive MMEDs (global warming, ozone depletion, or global pollution) is at least a decade away. Many of the anticipated effects may not be obvious in our lifetimes. White-band disease and CRB have caused great destruction on coral reefs (Williams & Bunkley-Williams 1990a; Bunkley-Williams *et al.* 1991; Glynn 1996). We need to document distinct, short-term indicators of long-term changes to emphasize the importance and reality of these changes. The loss of cay

Fig. 2 Diagram of a cross section of an average or typical transect of the coral cay and coral reef of Turrumotte Reef in 1974–75 (above) and 1992 (below). The wavy line represents sea level, the solid line with no stippled areas below represents solid substrate, the stippled area above sea level represents dead elkhorn coral, *Acropora palmata*, of the coral-reef rampart, and the stippled portions below sea level represent live elkhorn coral. No other corals or coral-reef organisms are shown to keep the figure simple for comparative purposes. The horizontal values have been divided by four so that adequate vertical distances could be incorporated to illustrate the elkhorn coral positions in the horizontal space available.



ramparts is a real, permanent, and measurable MMED-induced change which we predict will occur on many coral reefs.

Materials and methods

Study sites

Many of the reefs off south-western Puerto Rico possess well formed, emergent cays with plate ramparts (Figs 1,2) typical of these small islands throughout the Western North Atlantic. In the summer of 1992, we selected Cayo Media Luna (17°56.4'N, 67°02.8'W) (B in Fig. 1) and Cayo Turrumotte (17°56.3'N, 67°01.2'W) (C in Fig. 1), as representative of these high-energy cays.

Composition of cay ramparts

Using stratified-random sampling (Olhorst *et al.* 1988), we established 16 continuous line transects perpendicularly across the plate rampart (surface transects) (B and C in Fig. 1). The plate rampart of Turrumotte was divided into 10 64.5 m segments, and Media Luna into six 35.0 m segments. Transect sites within each segment were chosen using a random numbers table. Half of the transects were also arbitrarily chosen for vertical continuous line transects through the entire plate rampart at the apex (vertical transects). Surface transects were 11.0–39.5 m (average 19.1 m) long and vertical transects were 0.3–2.6 m (average 1.8 m) deep. Percentage cover transect data were arcsine-transformed and analysed using an unpaired Student's *t*-test (Sokal & Rohlf 1981). We mapped the cays and calculated the volume of the plate ramparts (Fig. 1) (see Appendix).

Available elkhorn coral on the reef

The bearings of the surface transects were continued across the adjacent 100 m of reef in the direction of wave energy (submerged transects) (B and C in Fig. 1, Fig. 2). Submerged transects extended out to depths of 2.1–18.3 m (average 6.8 m). Percentage cover transect data were arcsine-transformed and analysed using an unpaired Student's *t*-test (Sokal & Rohlf 1981).

Previous elkhorn coral available

The percentage of elkhorn coral cover prior to WBD and CRB damage was established with our previous field notes which detailed both the extent and height of this coral in 1974–75 (Fig. 2, upper), so that we could use similar methods to produce comparable measurements for the calculation of the coral volume, the extent of coral coverage was reconfirmed during the study with recognizable dead elkhorn bases, and part of the extent and the height were reconfirmed by previous descriptions of these reefs (Almy & Carrión-Torres 1963; Hernandez-Avila *et al.* 1977; Goenaga & Cintron 1979; Matta 1981). The volume of live elkhorn coral was calculated using percentage coral cover, average height of colonies and a 10:1 compaction ratio (the volume occupied by live, standing elkhorn coral on the reef was estimated to be 10 times the volume it would occupy in the rampart as broken plates) (see Appendix).

Active diseases on submerged transects

Obvious coral diseases [WBD, CRB, black-band disease (BBD) (Rützler *et al.* 1983; Edmunds 1991), and overgrowth by Lang's boring sponge *Cliona langae* Pang (Demospongiae: Hadromerina: Clionidae)(OCL)] were



Fig. 3 Underwater photograph of the underside of a colony of elkhorn coral *Acropora palmata* (Cnidaria: Scleractinia: Acroporidae) suffering from white-band disease (WBD) Laurel Reef off La Parguera, Puerto Rico, July 1995, 3 m depth. White band across centre of colony = active WBD, pigmented areas above band = live coral, dark area below band = dead surface where tissue has been removed by WBD and bare skeleton has been covered by algal growth. Photocredit: Andrew W. Bruckner.

counted and measured within 10 m of either side of the submerged transects (20 × 100 m quadrat). Sizes of the areas were directly measured and recorded by scuba divers. We included both areas recently affected by tissue loss from BBD and WBD (indicated by bare, white skeleton) and associated dead areas (colonized by filamentous algae) in measuring the area affected by these diseases.

Condition of elkhorn coral on other Western Atlantic reefs

We solicited reports of CRB and other reef damage by publishing and distributing summaries of disturbances

and questionnaires to biologists and environmentalists throughout the Western North Atlantic (Williams *et al.* 1986, 1987, 1991, 1992, 1994, 1996; Williams & Williams 1987a,b; Williams & Bunkley-Williams 1989, 1990a,b,c). Reports concerning the 1986–88 CRB and related sources of coral-reef destruction were collated and analysed (Williams and Bunkley-Williams 1989, 1990a).

Results

Composition of cay ramparts

The plate rampart of both cays (Figs 1,2) was almost entirely elkhorn coral [$87.7 \pm 7.39\%$ ($X \pm 1$ SD) of the surface, and $98.4 \pm 1.04\%$ ($X \pm 1$ SD) of the internal composition]. The percentage cover of elkhorn coral in surface transects on Turrumote ($X \pm 1$ SD = $88.7 \pm 4.6\%$) and Media Luna ($X \pm 1$ SD = $86.0 \pm 10.9\%$) were not significantly different ($t = 0.478$, d.f. = 14, $P = 0.6397$). Similarly, vertical transects did not differ ($X \pm 1$ SD = $98.4 \pm 1.34\%$ and $98.3 \pm 0.44\%$ for Turrumote and Media Luna, respectively, $t = 0.506$, d.f. = 14, $P = 0.6308$). However, vertical transects did differ from surface transects ($t = -6.05$, d.f. = 22, $P = 0.0001$). Previous studies estimated the composition of plate ramparts by using surface examination (Hernandez-Avila *et al.* 1977), but ignoring subsurface composition underestimates the amount of elkhorn in plate ramparts. Neither percentage cover of fire corals *Millepora complanata* and *Millepora alcicornis* (Cnidaria: Milleporina: Milleporidae) nor Lang's boring sponge differed on the two reefs ($t = 0.333$, d.f. = 14, $P = 0.7442$ and $t = 0.872$, d.f. = 14, $P = 0.3978$, respectively). The volume of elkhorn coral in the cay ramparts was 3600 and 12 800 m³, respectively (see Appendix).

Available elkhorn coral on the reef

Live elkhorn coral covered only $0.3 \pm 0.7\%$ ($X \pm 1$ SD) of the area of the submerged transects; average height of live colonies was 0.25 m (0.1–1.1 m) (Fig. 2, lower). Most submerged elkhorn coral skeletons have been removed by storms and bioerosion. The shallow (1–5 m) fore reef zones of these two reefs are now almost devoid of any live scleractinian corals ($2.7 \pm 2.7\%$) ($X \pm 1$ SD) or fire corals ($2.0 \pm 2.3\%$) ($X \pm 1$ SD). The present volume of live elkhorn coral in front of Media Luna and Turrumotte cays was 7 and 14 m³, respectively.

Previous elkhorn coral available

The former volume of the elkhorn coral thickets in front of Media Luna and Turrumotte cays was calculated to have been 11 000 and 34 900 m³, respectively (Fig. 2, upper).

Active diseases on submerged transects

Lang's boring sponge covered $10.8 \pm 5.3\%$ ($X \pm 1$ SD) of the submerged transects and was eroding hard substratum and dead and live stony coral colonies. Lang's boring sponge has not previously been so abundant and attacking live stony corals (Goreau & Hartman 1963; Vicente 1987). It is now very abundant on all of the reefs around La Parguera, Puerto Rico. This sponge seems to be a threat to live stony corals in our study area. White-band disease occurred commonly on the few remaining colonies of elkhorn (8.5%)(Fig. 3) and staghorn corals, *Acropora cervicornis* (Lamarck) (20.5%), in the quadrats. WBD and associated damage averaged 20.9% of the surface of affected elkhorn coral colonies and 11.8% of affected staghorn coral colonies. Black-band disease and associated tissue loss from BBD affected 0.4% and OCL 1.0% of the live colonies in the quadrats, and covered 49.4% and 50.2% of the surface of affected colonies, respectively. The growth forms of many of the colonies of elkhorn coral we examined were more bulbous and massive, and staghorn branches more twisted, curved, thickened and occasionally massive, than has been described for these species (Bak 1983; Peters *et al.* 1986).

Condition of elkhorn coral on other Western Atlantic reefs

The reports of CRB, WBD and other reef damage that we have received suggested that CRB and WBD have severely reduced the abundance of elkhorn coral throughout much of the Western North Atlantic coral reefs (Gladfelter 1982; Peters *et al.* 1983; Williams & Bunkley-Williams 1990a; Bythell & Sheppard 1993; Aronson & Precht 1997; Cervino *et al.* 1998). Bruckner *et al.* (1997) suggests that snail predation alone can eliminate the remaining colonies of elkhorn coral. We are in the process of assessing the extent and severity of coral-reef disease disturbances in cooperation with other laboratories and scientists (Cervino *et al.* 1998; Goreau *et al.* 1997).

Discussion

The former existing volume of live elkhorn coral in front of Media Luna and Turrumote cays was 305% and 272%, respectively, of the present measured volume of elkhorn coral in the plate ramparts (Fig. 2, upper). This was more than enough elkhorn coral to build the plate ramparts during a major storm. The plate rampart may not be formed by accretion, but rather destroyed and created anew with the skeletal coral materials available during each major storm which directly affects the reef (Glynn *et al.* 1964; Hernandez-Avila *et al.* 1977; Stoddart & Steers

1977; Armstrong 1981; van Duyl 1982). The present volume of live elkhorn coral in front of Media Luna and Turrumote cays is 0.1% and 0.2%, respectively, of the volume of elkhorn coral in the cay ramparts (Fig. 2, lower). Obviously, this amount cannot replace the plate ramparts. Additionally, previous major storm waves were dampened by the shallow elkhorn thickets before reaching the plate rampart. Future major storms will strike the plate rampart unimpeded. No elkhorn coral replenishment materials will be available. We predict that increased storm wave force and lack of replenishment skeletal coral materials will immediately reduce and eventually remove the cay ramparts. We also predict that these plate ramparts will eventually be permanently lost, allowing high wave energy to wash over the reef and reach inshore areas.

Live elkhorn coral now covers only 0.4% of the previous area occupied by this coral. The present volume of live elkhorn coral is only 0.05% of the former volume. The abundance of WBD we found in elkhorn coral suggests that the amount of this coral on the reef will continue to decline. The fore reefs that we studied appear to be dying (Fig. 2, lower). We estimate that the amount of WBD damage was more than sufficient to further decrease the abundances of elkhorn coral and staghorn corals; and BBD and OCL were sufficient to reduce the abundance of nonacroporid stony corals. This trend has continued since the study and many new and devastating coral-reef diseases have emerged (Cervino *et al.* 1998; Goreau *et al.* in review). The predominant process occurring in the fore reefs that we studied was bioerosion [Lang's boring sponge alone covered more than twice the area of all live corals (stony and fire)]. The aberrant growth forms we found in elkhorn and staghorn corals may also indicate deteriorating conditions on these reefs. White-band disease and CRB are expected to prevent any significant recovery of elkhorn coral, and thus replenishment of coral reef cay ramparts (Williams & Bunkley-Williams 1990a).

Conclusions

From the reports of CRB and other sorts of reef damage (Cervino *et al.* 1998; Bunkley-Williams *et al.* 1991; Williams *et al.* 1986, 1987, 1991, 1996; Goreau *et al.* 1997), we conclude that the supply of rampart-building corals may also be threatened on many high energy reefs in the tropical Western Atlantic. We anticipate that many of these reefs will lose cay ramparts when storm damage exceeds the rate of supply. Rubble ramparts occur on many Indo-Pacific coral reefs, and are a component of the most stable cays (McLean & Stoddart 1978; Harmelin & Laboute 1986). Branching corals in the Indo-Pacific, including *Acropora* spp., were the most affected by CRB

(Glynn 1983; Williams & Bunkley-Williams 1990a; Williams & Bunkley-Williams 1996, Bunkley-Williams *et al.* 1991). White-band disease also occurs in the Indo-Pacific (Williams & Bunkley-Williams 1996), although we do not know if it has affected these acroporids as drastically as those in the Atlantic. If so, coral reef cay ramparts in the Indo-Pacific may also eventually be in jeopardy.

The loss of cay ramparts may be the first obvious and permanent structural change caused by major ecological disturbances on the coral reef ecosystem. Besides being an obvious indicator of global change, the loss of cay rampart protection will alter coral reefs, back-reef and inshore environments, and shore lines.

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Appendix

Calculation of the volume of elkhorn coral in the plate ramparts. Subscript 1–10=transect points, b =beginning of plate rampart, e =end of plate rampart, L =Transect distance along plate rampart from west to east, H =Height of plate rampart, W =Width of base of plate rampart, P =% of elkhorn coral in plate rampart (average percentage in surface transects+average percentage in vertical transects/2).

$$P[L_1 - L_b \left[\frac{\pi H_b^2 + H_b W_b + \pi H_1^2 + H_1 W_1}{4} \right] + L_2 - L_1 \left[\frac{\pi H_1^2 + H_1 W_1 + \pi H_2^2 + H_2 W_2}{4} \right] + [\text{cont. to } e]$$