

COMMENTARY

WIDESPREAD INCIDENCES OF CORAL REEF BLEACHING IN THE 1980s: IS  
THERE A CONNECTION WITH GLOBAL WARMING?

by

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## INTRODUCTORY PARAGRAPH

Scleractinian corals and their symbiotic dinoflagellate algae build massive, wave resistant coral reefs that are preeminent in shallow tropical seas. This mutualism is especially sensitive to numerous environmental stresses, and has been disrupted frequently in tropical biogeographic regions during the past decade. Increased seawater temperatures have been suggested as the most likely cause of coral reef bleaching. These recent, large scale disturbances coincide with the anticipation of the 'greenhouse effect' and global warming. The observed bleaching events have been suggested as the first indication of global warming, reminiscent of 'the canary in the coal mine'. This article describes recent bleaching events, their geographic extent, possible link with sea warming and other environmental stresses, and some ecological effects. Finally, it offers some speculation on the fate of coral reefs should planet Earth enter a sustained period of warming.

Four coral bleaching complexes (a series of time-related bleaching events, cf. 1) in the 1980s have attracted unusual attention, in part because of their unprecedented scale, frequency, and association with a period of suspected global warming (1-5). This spate of disturbances has resulted in numerous newspaper articles, the publication of popular and technical articles, the convening of special international sessions and workshops, and even two hearings in the United States Senate. Just as explanations of global warming usually attribute increasing temperatures during the 1980s to higher concentrations of atmospheric CO<sub>2</sub> and other 'greenhouse gases', explanations of coral bleaching commonly invoke periods of anomalously high sea water temperatures, which are often equated with global warming. However, neither hypothesis is consistent with all observations and, therefore, both have met with controversy (1, 6-8).

#### NATURE AND EXTENT OF CORAL REEF BLEACHING

Coral bleaching occurs when photosymbiotic corals lose or expel a major portion of their dinoflagellate (zooxanthellae) flora, when the concentration of photosynthetic pigments in zooxanthellae declines drastically, or some combination of the two. At such times, the coral host pales or bleaches due to the low concentration of plant pigments and the increased visibility

of the coral's white calcareous skeleton. Bleaching is not limited to reef-building, scleractinian corals, but also occurs in a variety of zooxanthellate species, including for example hydrocorals, alcyonarians, sea anemones, soft corals and bivalve molluscs (1). Some sponges that host photosynthetic cyanobacteria also bleach (9).

Bleaching is a stress reaction that can be induced by many conditions, e.g. high and low water temperatures, high fluxes of visible and ultraviolet radiation, prolonged aerial exposure, freshwater dilution, high sedimentation and various pollutants (1, 3, 4). High temperature and high light increase the production of active oxygen species such as  $O_2^-$  and  $H_2O_2$  (10, 11). Resultant oxygen toxicity may be the cause of bleaching at the cellular level. Additionally, the concentration of UV-blocking pigments decreases at high temperatures suggesting another stress to corals and zooxanthellae (11). The sudden loss of zooxanthellae greatly impacts the coral animal because these photosynthetic symbionts supply up to 63% of the coral's nutrition (12), and also because they facilitate calcification. If corals do not regain their dinoflagellate flora they usually die. If bleaching is not too severe corals often recover, however, the extent of zooxanthellae loss and coral tissue damage that can be tolerated is unknown.

In 1979-80, coral bleaching and mortality were reported in 4 areas of the Pacific Ocean and in 2 areas of the Caribbean Province (Fig. 1). Except for the extensive disturbance observed

in the Ryukyu Islands, the 1979-80 bleaching events were restricted to specific sites, i.e. to particular islands or reefs. In 1982-83, a remarkably strong El Niño-Southern Oscillation (ENSO) event, perhaps the strongest in 200 or more years (3, 13), resulted in intense and widespread ocean warming in the equatorial eastern Pacific. Severe bleaching accompanied the 1982-83 ENSO, resulting in mass mortalities of corals in Costa Rica, Panama, Colombia and Ecuador (14). Overall, disturbances were reported in 1 region (Panamic Province) and at 12 sites in the Indo-Pacific Province and at 5 sites in the Caribbean Province during the 1982-83 ENSO event. Several sites affected in the early 1980s (in the Great Barrier Reef region of Australia and at 5 other sites) were again disturbed within one year of the moderate ENSO event of 1987. During the 1986-88 bleaching complex 12 new sites were disturbed, including reefs throughout the Red Sea and nearly the entire extended Caribbean region, including the Flower Garden Banks (Gulf of Mexico) and Bermuda (in 1988, 15). The most recent coral bleaching events (1989-90) have been confined largely to the Caribbean region with severe effects to November 1990. Bleaching in 1990 has led to greater coral mortalities in parts of the Florida Keys and on the southern Puerto Rican coast than was observed in 1987.

#### LINK TO HIGH SEA TEMPERATURE

Coral bleaching and mortality result from many different stressors (16, 17). If sea warming is an important cause of the recent disturbances then it is necessary to determine if there has been a significant increase in the frequency of mortality

events. If so, the strength of the warming-bleaching relationship must be assessed. Brown (18) and Coffroth et al. (4) examined the ENSO-related coral bleaching and mortality events of 1982-83 on a global scale and concluded that the majority (70%) were probably attributed wholly or in part to elevated water temperatures. Other ENSO-related causes of coral mortality included coral exposure due to sudden sea level drops and high rainfall (with reduced salinities) that resulted from increased cyclonic activity. Five of 9 non-ENSO associated mass coral mortality events observed during 1979-85 also were attributed to high temperature stress (18). Of 29 mass coral mortalities reported from 1876-1980, 21 events were attributed to cyclones and heavy rainfall and none to sea warming (4). Thus, the historical record of severe disturbances supports a connection between anomalously high sea temperatures and coral mortalities only in recent years. However, because the causal relationships cited in these studies often are based on anecdotal or subjective observations, the strength of such an argument is seriously limited.

Severe disturbances to coral reefs at several sites in the tropical eastern Pacific were closely associated with the timing and intensity of the 1982-83 ENSO event (3). Bleaching resulted in 50% coral mortality on Costa Rican coral reefs, 75-85% mortality on Panamanian reefs, and 97% mortality on coral reefs in the Galapagos Islands (14). The 1982-83 ENSO was exceptionally strong and coincided with a near-decadal warming period in the southeastern Pacific (3, 19). Although bleaching

events in the western Pacific and Caribbean were often associated with high sea temperatures, the temperature anomalies in those areas were usually slight and only weakly coincident with coral bleaching (4). Many workers attributed the 1987 Caribbean-wide bleaching event to sea warming, often accompanied by doldrum-like conditions, but a lack of long-term, high quality temperature observations from the disturbance sites often weakened such interpretations (20). Moreover, an analysis of largely offshore sea temperatures did not detect significant warming in the Caribbean Sea in 1987 (8). More recent analyses have demonstrated significantly higher ocean temperatures off Hawaii ( $1^{\circ}\text{C}$  above the long term mean) during the 1986-87 coral bleaching events there (21), and at 5 of 7 sites ( $0.4^{\circ}$ - $1^{\circ}\text{C}$ ) that experienced bleaching in the Caribbean during the past decade (22).

Experimental studies quantifying zooxanthellae expulsion from corals and the loss of photosynthetic pigments at elevated temperatures offer additional support for the hypothesis that slightly elevated sea temperatures maintained for several weeks could have caused many of the coral bleaching events observed in recent years (21, 23-25). Bleaching can be induced in 1-2 days by temperature elevations of  $3-4^{\circ}\text{C}$  above warm summer conditions or in several weeks by temperature elevations of only  $1-2^{\circ}\text{C}$  above summer conditions (21). An El Niño simulation experiment conducted in Panama showed that a temperature increase of  $2^{\circ}\text{C}$  over 8-10 weeks duplicated the time course of physiological changes and mortalities of corals and obligate coral crustacean

symbionts observed in the field during the 1982-83 El Niño disturbance (25). Increased bleaching of the upper portions of coral colonies indicates that high light levels and high temperature may have an additive or synergistic effect in some instances (11).

Consequently, many coral bleaching and mortality events have been linked with sea warming during the 1980s. But the reality of sustained, widespread sea warming has not been substantiated, and the link between recent sea warming events and global warming is problematical because of the large variations in temperatures observed over the instrumental record and the time intervals selected for analysis by different workers (6,7).

#### ECOLOGICAL DISRUPTIONS

The potential physiological and ecological effects of bleaching are numerous. Early responses in the coral host often include an increase in respiration rate, declines in coral protein, lipid and carbohydrate, a weakening of tentacular movement, a decrease in skeletal growth, gonadal regression and tissue necrosis (21, 24-30). Parasitic and mutualist species that require healthy corals for shelter and sustenance suffer when their hosts are stressed by elevated thermal conditions (21, 31, 32). The near total mortality of crustacean guards in branching corals affected by the 1982-83 El Niño event in Panama resulted in predatory attacks by Acanthaster planci on 100-200 year old massive corals. Before the warming event, the old massive colonies were surrounded and protected from sea star

(A. planci) predators by continuous stands of branching corals with their crustacean mutualists, which effectively excluded the predators. This secondary predation is still in progress, 7 years after the initial disturbance (3).

Additional long-term effects can lead to reduced cover of important reef-building species and to increased abundances of species that erode reef frameworks. In the Pacific Ocean, many of the faster-growing, branching coral species were more susceptible to bleaching and mortality than slower-growing, massive species (3, 33, 34). If numerically abundant, rapidly accreting corals are replaced by slower-growing corals or non-reef building benthos, such as fleshy algae, sponges, soft-bodied coelenterates and tunicates, then reef growth would be retarded. While important reef-building species were affected during the bleaching disturbances in the Caribbean Sea, there was no clear difference in susceptibility of fast and slow-growing corals (1). When bleached corals die, space becomes available and is often colonized by non-reef building organisms. Dead reef frameworks also provide shelter and grazing surfaces for many potentially destructive animals such as infaunal (boring sponges and mussels) and external (sea urchins and fishes) bioeroders (35, 36). On eastern Pacific coral reefs that suffered high coral mortality in 1982-83, bioerosion now exceeds net carbonate production and threatens to reduce firm reef structures to sediment (36, 37). Preliminary results on coral community recovery following mass bleaching and mortality events reveal highly variable rates: coral cover on an Indonesian reef attained

50% of its former level after 5 years (34), but in the Galapagos Islands virtually no recruitment to coral reefs has been observed after 7 years (37).

#### SPECULATIONS

If tropical seas warm 1-2°C over the next century, coral reefs could be impacted in several ways. Because reef-building corals live so near their upper thermal tolerance limits, sea warming over a period of 50 years or less (38) may cause the extinction of many coral species. This prediction is based on observations in Hawaii (21), which suggest that much longer time periods than a few decades would be necessary for the selection of high thermal tolerance in long-lived corals. Small, geographically isolated populations would be especially susceptible to such changes. For example, three reef-building coral species probably were extirpated from the eastern Pacific as a result of the 1982-83 ENSO warming event (3).

Some reef corals in the Arabian Gulf can withstand both very high and low temperatures (13-36°C, 39), indicating that given time certain populations can adapt to temperature extremes. However, corals in the southern Arabian Gulf (Straits of Hormuz) suffered mass bleaching and 50% mortality in 1990 (40). This suggests that even some corals adapted to extreme thermal conditions can be severely affected by sea warming over prolonged periods.

An additional burden to thermally-stressed corals could be

imposed by heat resistant, non-photosymbiotic organisms that would compete with, prey upon or bioerode surviving corals and coral frameworks. Rising sea level predicted to accompany global warming could have variable effects on reef growth depending upon particular regional settings. For example, Greenhouse sea level rise may rejuvenate the upward growth of reef flats on the Great Barrier Reef complex, Australia (41), but could drown coral reefs and increase sedimentation, light attenuation and nutrient loading in the Caribbean Sea (42, 43). The Australian scenario of accelerated reef growth assumes that fast-growing, branching corals would be favored on flooding reef flats, but it fails to account for observations indicating that branching corals are the most susceptible to temperature increases (33, 34), which may accompany sea level rise.

In light of the persistence of scleractinian coral reef ecosystems through numerous warming periods over geologic time, it is highly probable that many reef-building coral species would survive global warming over the projected atmospheric temperature increases of 1.5-5°C during the next 50-100 yrs (7). According to Emiliani et al. (44), about 20% of the late Cretaceous reef-building coral genera survived an even more abrupt temperature rise, ~10°C over a few months, that caused global biotic devastation at the Cretaceous-Tertiary boundary. Rapidly rising sea level would certainly have an initially disturbing effect, but with the eventual stabilization of sea level, a latitudinal shift in reef coral distribution may result in more active reef building at higher latitudes than at present.

## CONCLUSION

Whether or not the coral bleaching complexes of the 1980s have been caused by global warming is a critically important yet currently unresolved question. However, the numerous recurrent, large scale coral bleaching and mortality events observed in recent years are not theoretical. Like the destruction of tropical rain forests, the world's coral reef ecosystems are also facing major disruptions. Indeed, the deterioration of some coral reefs has been caused by increased sedimentation and eutrophication associated with rainforest destruction (45-47). Although much of the available evidence, however varied, points to increased seawater temperatures as the most likely cause of coral reef bleaching, many bleaching events have occurred from unknown causes. Long-term monitoring, and comparative and experimental studies will be required to understand the reason(s) for these disturbances and to gauge their potential impacts on the biosphere. Only with such knowledge can any remedial measures be contemplated.

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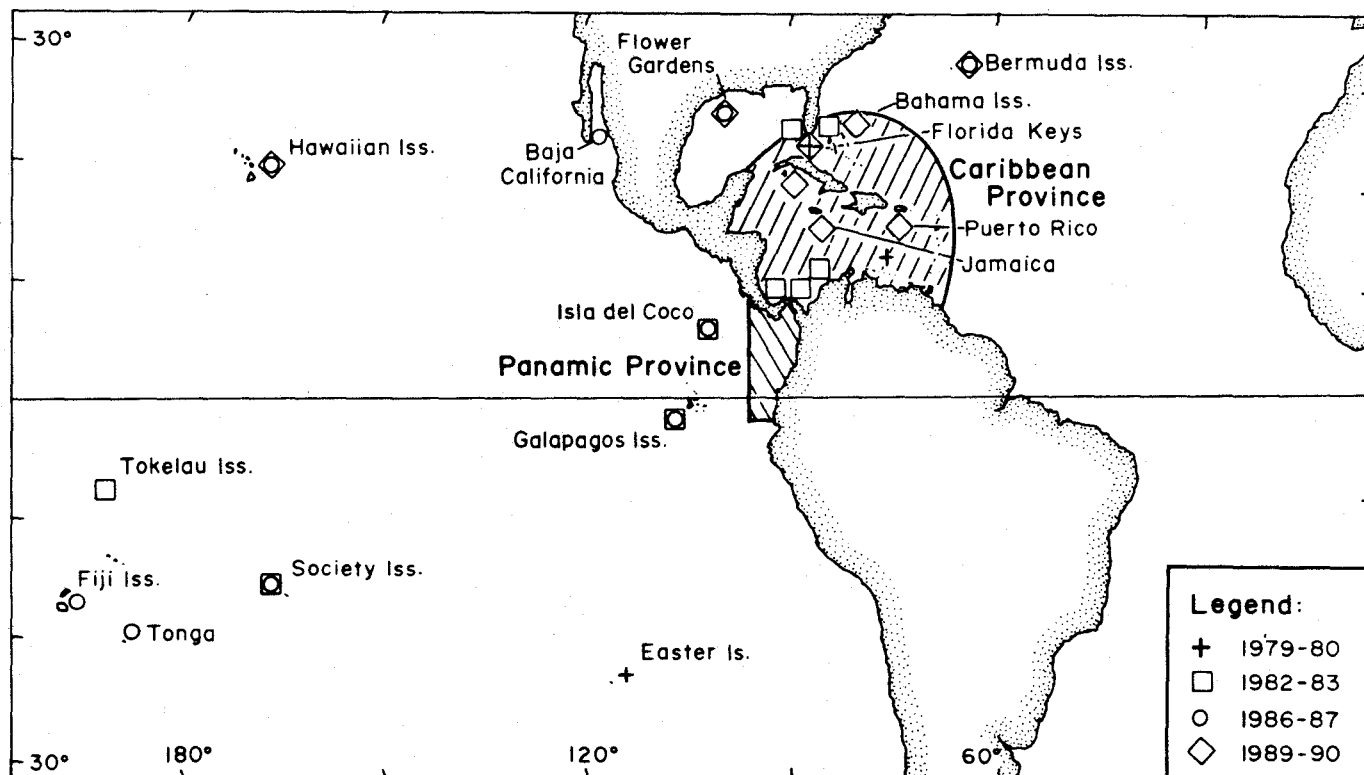
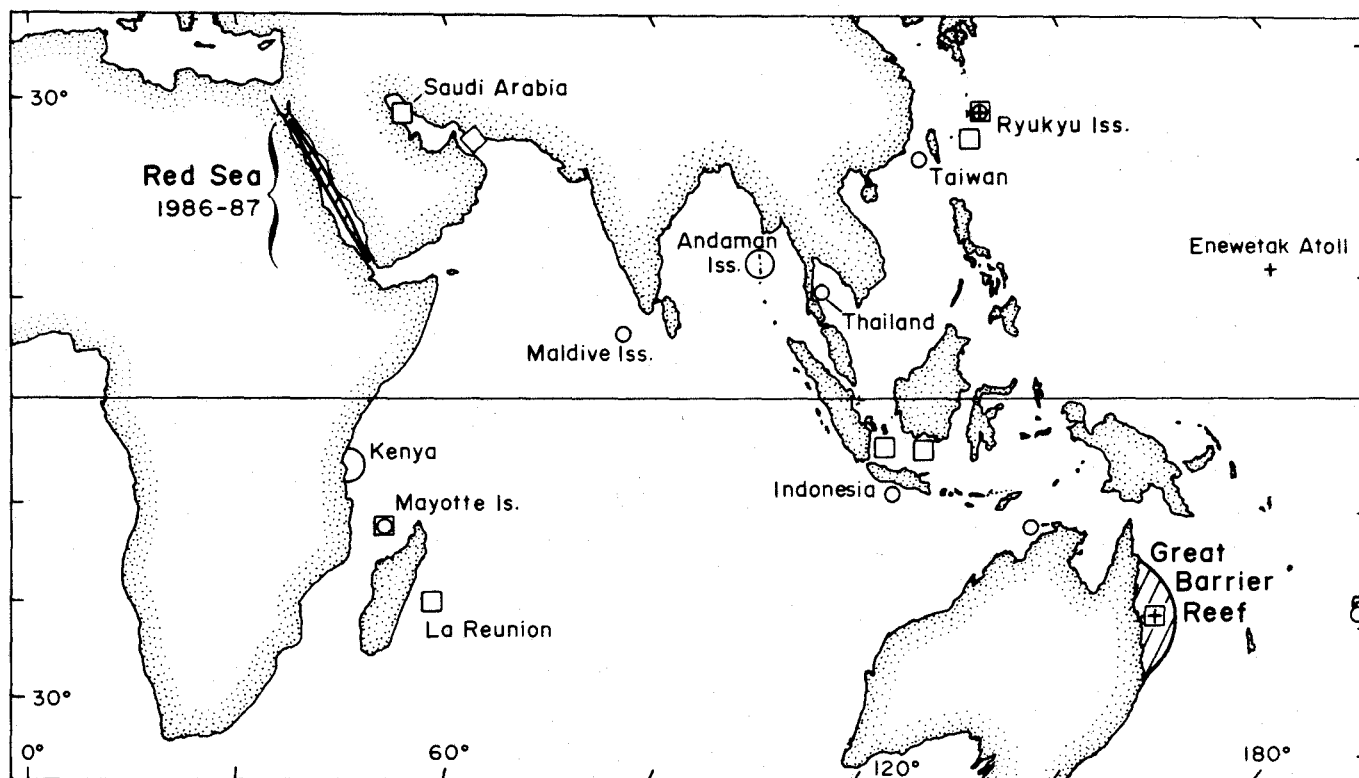
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## FIGURE CAPTION

Fig. 1. Location of coral reef bleaching sites reported during the four bleaching complexes in 1979-80, 1982-83, 1986-87 and 1989-90 (modified after E.H. Williams, Jr. and L. Bunkley-Williams, 1 and pers. comm.). The 1990 record for the Sultanate of Oman was reported by R. Salm (40). Large areas of coral bleaching (diagonal lines) included the Panamic Province (1982-83), Red Sea, Great Barrier Reef region, and a major portion of the Caribbean Province (1986-87).



**Legend:**

- + 1979-80
- 1982-83
- 1986-87
- ◇ 1989-90