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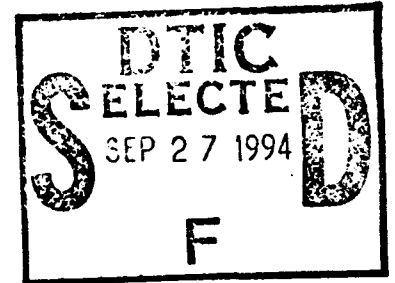# PROJECT REPORT

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CORRELATION OF CORAL BLEACHING EVENTS AND REMOTELY-SENSED
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CORRELATION OF CORAL BLEACHING EVENTS AND REMOTELY-SENSED SEA SURFACE TEMPERATURES

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Abstract

In the 1980s and early 1990s, coral reef bleaching events of unprecedented frequency and global extent were observed. Elevated water temperature is suspected as the primary causal stress of mass bleaching events from this period. The relationship between sea surface temperatures (SSTs) and coral bleaching events was investigated using National Oceanic and Atmospheric Administration (NOAA) Multi-Channel Sea Surface Temperature (MCSST) satellite imagery from 1982-1992. Nighttime MCSST weekly averages were compared with moored-buoy temperatures for sea-truthing the satellite. Average errors from 11 individual buoy comparisons throughout the tropics were found to be approximately 0.5°C when satellite data contaminated by volcanic aerosols (*El Chichón* 1982/83, Mt. Pinatubo 1991/92) were discarded. Confirmed satellite SST data were applied to bleaching events at Bermuda (1988, 1991), Tahiti (1984, 1987, 1991), and Jamaica (1987, 1989, 1990), with a non-bleached site off Belize selected as control. MCSST data showed elevated SSTs coincided with bleaching events both in onset and duration. A satellite temperature bleaching "threshold" was produced for the three sites, and histogram analyses of MCSST temperatures revealed increased periods of high SSTs correlated with the occurrence of mass bleaching events. An MCSST *Degree Heating Weeks* (DHW) bleaching index was developed for the Belizean and Jamaican reef sites. A cumulative heating stress of 26 DHW is proposed as the threshold for mass reef bleaching at Belize and Jamaica.

Keywords: corals, coral bleaching, remote sensing, sea surface temperatures (SSTs)

Preface

This study deals with the impact of physical environmental parameters on living organisms. A brief background on coral classification, structural forms, and growth rates, with a supplementary categorical table of coral species mentioned in this study will be presented.

Corals belong to the phylum *Coelenterata*. The basic structure of the living part of a coral (the polyp) is similar to an anemone. Polyps are generally cylindrical in shape, the opening fringed by usually retractable tentacles leading down into the gastrovascular cavity. Numerous polyps grow together to form colonies. All coral varieties build some sort of calcium-based (calcareous) skeleton. Hard corals build solid skeletons around their polyps, while soft corals generate skeletal fragments within their tissues, giving them a fleshy appearance. The predominance of corals discussed in this work and all species mentioned are hard corals, which include hydrocorals and scleractinians. The latter variety of coral is known as true or stony coral, belonging to the Class *Zoantharia*.

There are four major forms of corals--branching, encrusting, massive (large, rounded bodies), and foliaceous. These different forms grow at different rates; branching varieties such as *Acropora* species are the fastest, in contrast to the slow-growing *Montastrea annularis*, a massive coral. Corals satisfy their nutritional and oxygen requirements primarily through intracellular zooxanthallae, an algal symbiont. In addition, a coral will normally extend its tentacle to feed on plankton, especially at night (Wood, 1983). The following is a table of coral species mentioned in this work

and their classifications.

Table I Classifications of coral species and genera referred to in text.

Hydrocorals	Scleractinian (stony) Corals
Millepora	Branching:
Millepora alcicornis	*Acropora*
("fire" corals)	*Acropora palmata*
	Pocillopora
	Massive:
	Montastrea annularis
	Diploria labyrinthiformis
	Gardineroseris planulata
	Pavona varians
	Porites lobata

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Introduction

The coral reef is a unique and very rich ecosystem which supports a vast array of animal and plant species. The fisheries dependent on coral reefs have supported many cultures for ages. Corals form the structural and ecological foundation of the reef system. Coral reefs flourish mainly in the tropical latitudes, extending at most to 30° north or south of the Equator in only a few cases (Wood, 1983).

Every coral species, as well as numerous other reef inhabitants, maintains a special symbiotic relationship with a microscopic organism called zooxanthallae. Zooxanthallae are photosynthetic algae which live by the millions in the tissues of the coral. These organisms provide their hosts with oxygen and a portion of the organic compounds they produce through photosynthesis. In return, the coral provides the zooxanthallae with an environment highly conducive to autotrophic growth: one rich in carbon dioxide and other animal waste products (Bunckley-Williams and Williams, 1990). When stressed, many reef inhabitants have been observed to expel their zooxanthallae *en masse*. Alternatively, the zooxanthallae may lose their photosynthetic chlorophyll pigments, or a combination of expulsion and loss of pigments may take place in response to environmental stress (Jaap, 1985). The polyps of the coral are left bereft of pigmentation and appear nearly transparent on the animal's white skeleton. This phenomenon is normally referred to as coral bleaching.

Bleaching, however, is not an all-or-nothing event, and different varieties of corals exhibit a full range of bleaching responses to stress that may or may not leave a coral white in appearance (Goreau, personal communication). The term "mass

bleaching" has been used recently to describe a severe bleaching event of large geographic extent affecting numerous species of corals and multiple depth ranges (Goreau, 1992). High levels of stress tend to induce these dramatic events, such as the high mortality bleachings of many reefs off Panamá's Pacific coast following the severe *El Niño* of 1982-83 (Glynn, 1984). Less severe cases of bleaching might only affect partial portions of a colony, certain depth ranges of a reef, or a few coral varieties (Jaap, 1985). Spotty, slight bleaching or partial paling is common when the level of environmental stress is low (Gates, 1990).

More severe bleaching events have more dramatic long-term effects on the coral. Strong events radically alter normal metabolic functions, affecting calcification, reproduction, and tissue maintenance. When expulsion of zooxanthallae takes place, the affected reef organisms are forced to rely on heterotrophic mechanisms to procure nutrients (Jaap, 1985). Corals maintain the ability to feed on drifting plankton by extending tentacles from their polyps. Following some bleaching events, observers have noted the nearly transparent appearance of these tentacles when the coral is seen feeding at night (Bunckley-Williams and Williams, 1990). This ability of the coral to feed itself in the absence of zooxanthallae may be very important to its survivability during and after a bleaching event. Recovery of zooxanthallae may be possible through reinfection from neighboring corals or potentially via free-living waterborne varieties of the alga (Buddemeier and Fautin, 1993). Recovery rates, however, appear to differ greatly from species to species, and time to full recovery of symbiotic algae may take as little as 2 months or as much as a year (Jokiel and Coles, 1977; Lang *et*

al., 1992). When the level of environmental stress is high and sustained however, death of the coral may result (Glynn, 1984).

Normally, low levels of bleaching are natural phenomena of the reef environment (Gates, 1990). Seasonal bleaching has been observed on many reefs and is generally slight; 98% of coral colonies bleached during 1988 in Jamaica were categorized as 1-25% bleached (Gates, 1990). A similar situation has been documented for the central and northern Great Barrier Reef, where recurrent low level bleaching and coral growth records suggest corals are stressed every summer during the warmest times of the year due to a possible combination of water temperature and ultra-violet light stresses (Oliver, 1985).

Mass bleaching events, however, exceeding normal seasonal or slight bleachings have been observed with alarming frequency since 1979 (Glynn, 1993). The severe bleaching events observed from 1979 to the present appear to many biologists as a signal of global change. The frequency and scale of those events suggest a large change may be taking place in the world's coral reefs. Such dramatic reef bleaching events are unprecedented within the history of scientific observation of reef ecosystems. Mass bleaching was not observed even during the intense periods of reef research and study in the 1960s and 1970s following the advent of the Self Contained Underwater Breathing Apparatus (SCUBA). The 1980s, however, brought change to the world's reefs. At least 60 major coral reef bleaching events (involving coral mortality) were reported from 1979 through 1990, compared to 3 events of similar magnitude reported for the previous 103 years (Glynn, 1993). Recently,

increasing threats to coral reef systems include escalated anthropogenic stresses and possible natural or human-induced climate changes. Regardless of what the sources of these changes are, reefs around the world have responded in negative ways to increased environmental stress over the past 14 years. It has been argued that sensitive coral reef ecosystems may work as ecological alarms, warning us of large scale environmental change (Bunckley-Williams and Williams, 1988; Brown, 1987; Glynn, 1993).

The bleaching events reported prior to the 1980s were generally attributed to localized phenomena such as major storm events, severe tidal exposures, sedimentation, rapid salinity changes, pollution, or thermal shock (Glynn, 1993). The events since 1980 have not been so easily explained. Numerous laboratory studies have shown a direct relationship between bleaching and water temperature stress (Coles *et al.*, 1976; Jokiel and Coles, 1977; Glynn and D'Croz, 1990; Gates *et al.*, 1992). Elevated water temperatures are suspected in a number of the major events of the 1980s and 1990s (Bunckley-Williams and Williams, 1990; Glynn, 1988; Brown and Suharsono, 1990).

Objectives and Met.

This research explores the relationship between elevated sea surface temperatures (SSTs) and coral bleaching events. No reliable *in-situ* SST time series exist for many coral reef locations. Therefore, the primary data source for this study was National Oceanic and Atmospheric Administration (NOAA) Multi-Channel Sea Surface Temperature (MCSST) data collected by the Advanced Very High Resolution Radiometer (AVHRR) onboard a NOAA polar orbiting satellite from 1982 through 1992.

There were two major objectives of this study. The first objective of this project was to conduct a sea-truthing effort centered on moored-buoy SST comparisons with satellite data. Global SST images in the form of weekly averages of nighttime MCSST data were manipulated on the VAX workstations in the Cooperative Project in Oceanic Remote Sensing (CPORS) laboratory at the United States Naval Academy. Satellite-derived time series were produced at 1! buoy sites and then compared with the buoy records (see figures 1 and 2 for buoy locations). Buoy data were made available through NOAA, some via Internet from their Pacific Marine Environmental Laboratory (PMEL) in Seattle, Washington, and the remainder from their National Oceanographic Data Center (NODC) on CD-ROM.

The second objective of this project was to apply the confirmed satellite record to coral bleaching events at selected reef sites (see figure 1). Once the satellite performance had been validated for the appropriate periods, the MCSST record was used to investigate the relationship between elevated sea surface temperatures and

coral bleaching events at Bermuda, Tahiti, and Jamaica. Belize was selected as a control site based upon its latitudinal proximity to Jamaica and zero incidence of reported bleaching from Glover Reef, Belize (Glynn, 1993; M. Eakin, personal communication). MCSST extraction points for buoys and reefs are listed in Table II.

Table II MCSST extraction points for buoy comparisons and reef sites.

Buoys	Reef sites	MCSST Reef Location
25.9N, 89.7W	Bermuda	32.43N, 64.78W
26N, 93.5W	Tahiti	17.37S, 149.27S
23.4N, 162.3W	Jamaica	18.72N, 77.08W
2S, 110W	Belize	16.8N, 87.7W
2N, 110W		
8S, 110W		
0S, 124W		
2N, 140W		
0S, 169W		
2S, 165E		
2N, 165E		

Figure 1 MCSST image of Western Hemisphere centered on tropical belt. Buoy sites and reef sites are indicated.

Figure 2 MCSST image of Eastern Hemisphere centered on tropical belt. Location of 2 buoys used in sea-truthing indicated (+) at 2S, 165E and 2N, 165E.

Coral Bleaching

Reef specialists still do not fully understand the delicate symbiotic relationship between reef organisms and zooxanthallae. The exchange of oxygen and nutrients for carbon dioxide and respiration waste products is clearly understood, yet detailed intricacies of the complex relationship are still a mystery. How do different coral species respond to stress? What controls and influences the metabolism of a coral? What causes the relationship between the coral and zooxanthallae to break down? How do geographic location and ambient temperature range affect thermal tolerance? There are numerous questions that have yet to be addressed in research, but some accomplishments have been made that provide insight into the mechanisms of coral bleaching and affect the study of this phenomenon in relation to environmental stress.

a. The 1983 Equatorial Pacific Event

Coral reef bleaching was catapulted into the forefront of environmental concern with the near-destruction of many reefs following the exceptionally strong *El Niño* of 1982-83 (Brown, 1987; Coffroth *et al.*, 1990). An *El Niño* is one part of a major fluctuation in the normal coupling of the atmosphere and ocean in the tropical Pacific known as the *El Niño*-Southern Oscillation (ENSO). One of the oceanographic events associated with an *El Niño* is an intrusion of anomalous warm water into the eastern tropical Pacific. Normally, longshore winds and current patterns along the western coasts of North and South America induce upwelling and keep the thermocline relatively close to the surface. Upwelling brings cool, nutrient rich water to the

surface and is primarily responsible for increased levels of primary productivity (Bearman, 1991). During an *El Niño* event, warm water is transported eastward by a broadening of the northern equatorial countercurrent into the eastern tropical Pacific, suppressing upwelling and generating positive SST anomalies (Coffroth *et al.*, 1990). Extensive bleaching and reef mortality was observed at a number of reef sites in 1983 coincident with the period of highest SST values for the exceptionally strong *El Niño* event (Glynn *et al.*, 1988; Brown, 1987). The unfortunate demise of many corals and the apparent elimination of two hydrocoral species from the region (Glynn and DeWeerdt, 1991) following this occurrence brought the coral bleaching question into the scientific spotlight.

Original observations of the events of 1983 became commonplace in the reports of later bleachings. Dr. Peter Glynn, a reef biologist working at the Smithsonian Tropical Research Institute at the time, first observed bleaching on the Uva Island reef, Contreras Islands, Panamá in that year. In the mass bleaching that eventually spread throughout the eastern tropical Pacific, hydrocorals and branching scleractinians, especially *Millepora* and *Acropora* species, were the first hit and the most severely affected. Glynn observed bleaching in the Gulf of Chiriqui in early 1983, beginning in January and extending through April. In March, species of the hydrocoral genus *Millepora* had been eliminated from shallow portions of the reef, but were alive in deeper waters. By April, no living colonies of the hydrocoral could be found and large portions of reef cover made up primarily of pocilloporid corals had been bleached (Glynn, 1983). Other species were impacted differently. Massive reef

building corals such as *Pavona varians*, *Gardineroseris planulata*, and *Porites lobata* showed pronounced bleaching on their upper surfaces; while their sides and undersides kept their natural color. Some pocilloporid corals also exhibited a partial bleaching response, with only some pigmented streaking left on the undersides of their basal branches indicative of zooxanthallae presence. Glynn took specimens of the stricken corals from the reef and grew them in controlled laboratory conditions to study the physiological effect of bleaching on the corals.

After four weeks in the laboratory, he found that the pocilloporid specimens did not demonstrate any significant growth, while partially bleached massive colonies grew in captivity. Non-bleached corals from the Gulf of Panamá used as a control showed normal branch elongation and calcification. In addition to the reduced laboratory growth rates, bleached specimens in the field showed a significant reduction in mucus secretions and the presence of crustacean symbionts. Pocilloporid corals normally secrete mucus readily and are host to a number of 'crustacean guards'. Bleached colonies had only 9-10 associated crustacean symbionts, whereas healthy colonies on average had 22 crustaceans per colony (Glynn, 1983).

Ranking the susceptibility of different coral species to this event, Glynn found hydrocorals were the most susceptible, followed by pocilloporids and massive corals. Deep colonies of all coral varieties fared better early in the event, but were similarly affected in later stages of the bleaching. All corals killed by the bleaching were quickly covered over by macrophytic algae.

Concurrent with the bleaching observed in the Gulf of Chiriquí, an event of

equal if not greater severity was underway in the Galapagos Islands (Glynn, 1983).

Eventually, bleaching would show up off the coast of Costa Rica at Caño Island and

in the Gulf of Panamá (Glynn et al., 1988). The same patterns were observed at these

sites as had been seen in the Gulf of Chiriqui; hydrocorals were most severely

affected, followed by branching and then massive scleractinians (Glynn et al., 1988).

Another case of bleaching associated with the strong 1982/83 El Niño

took place on the shallow reefs in the Java Sea near Jakarta. Elevated SSTs from in-

situ observations (2-3°C higher than 1984, 1985, or 1986 temperatures) were observed

on the shallow reefs, followed four to six weeks later by bleaching of 70 species of

reef inhabitants from 33 genera. Acropora and Pocillopora corals were the most

severely affected. Total coral death eventually reached 80-90% on the Pari Island reef

flats. A possible interaction of increased ultra-violet radiation and seawater

temperatures was suggested as the cause of the bleaching (Brown and Suharsono,

1990; Glynn, 1984).

b. The 1987 Caribbean Event

A second major bleaching event took place in 1987 in the Caribbean Sea,

coincident with a mild ENSO event in that year (Brown, 1987). ENSOs are

commonly associated with conditions in the tropical Pacific only, but can impact

weather conditions worldwide. An ENSO event can cause doldrum-like conditions in

the Caribbean that may allow for increased solar radiation and heating (Glynn, 1993).

In late summer 1987, scientists, fishermen, and divers in the area began noticing large

white patches appearing on reefs. In August of that year, researchers were alerted to the occurrence of cloudy yellowish water surrounding some reef sites and obscuring the water column. Diving on the reefs, they found significant tracts of bleached corals, zoanthids, gorgonians, and sea anemones (Bunckley-Williams and Williams, 1988). It was later theorized that the yellowish brown clouds present in the waters covering large areas of the reef sites were actually made up of expelled zooxanthallae and their host epidermal cells (Williams, 1988). Bunckley-Williams and Williams (1988), two researchers from the University of Puerto Rico, began contacting marine labs, marine parks, and diving centers in order to ascertain the extent of the phenomenon. What they eventually discovered was astounding. Major bleaching had been observed throughout the Caribbean, beginning in June of 1987 at Bimini, Bahamas, and the Florida Keys. By July, Jamaica and southern Florida had been affected. From August through October, bleaching observations were reported from Culebra, Puerto Rico, the British Virgin Islands, Mona Island, the Flower Garden Banks off the Texas coast, the Dominican Republic, U.S. Virgin Islands, Lee Stocking Island in the Bahamas, Turks and Caicos, and Anguilla.

No one event seemed to follow an identical pattern in terms of onset, intensity, duration, species, or depths affected; nor was there any apparent regional trend in the spread of the bleaching. Only *Montastrea annularis*, an important reef builder, was almost universally reported as having been affected (92% of bleached sites). In general, bleaching was most severe in shallower depths, but was reported over the full range of habitats and depth range of zooxanthallate organisms (Bunckley-Williams and

Williams, 1988).

c. Potential Causes

A number of environmental conditions have been identified as causal factors in past coral bleaching events. Stresses such as aerial exposure of corals at exceptionally low tides or during anomalous low sea level periods, freshwater incursions, high or low water temperatures, increased levels of ultraviolet radiation, storm shock, turbidity, sedimentation, disease, or pollutants have all been implicated (Glynn, 1993). Coral bleaching events previous to the 1980s were typically of short duration, restricted to specific regions of a reef, and easily explainable as connected to one of the previously mentioned stresses (Williams and Bunckley-Williams, 1988). Since 1979, the numerous reported incidents of mass bleachings such as the 1983 and 1987 events that do not follow this pattern require an alternate explanation. One has yet to be thoroughly developed and proven.

During the 1983 *El Niño*, suppressed sea levels in the western equatorial Pacific led to aerial exposure of many reefs. Reef flat corals were severely exposed at low tides and eventually bleached and died. Two locations reporting bleaching of this nature were Nukunonu Atoll, Tokelau Islands in early 1983, and Moorea Island in French Polynesia in that same year (Glynn, 1984).

Bleaching connected to riverine outflows or submarine springs is usually due to the introduction of large amounts of freshwater onto a reef, identifiable by noticeable stress gradients leading to the freshwater source. Submarine springs and

rivers have been blamed for some localized bleachings in Jamaica (Goreau, 1992). Additional bleaching stresses connected to riverine sources include sedimentation from storm run-off or pollution delivered by the river plume outflow from human dwellings, farming, or construction (Goreau, 1992; Glynn, 1984; Brown, 1987).

"White band disease" was blamed for a number of cases of mortality of the reef builder *Acropora palmata* in the Caribbean in the 1980s (Brown, 1987). A causative agent has not been isolated, but a bacterium has been implicated. Disease was ruled out as a factor in the mass bleaching event of 1983 in the Pacific based on histological examinations of coral tissues (Glynn, 1985). The sudden onset and wide geographic extent of mass bleaching events across multiple species and depth ranges rules out a waterborne pathogen for the 1987 Caribbean event although the possibility of an airborne pathogen has not been totally abandoned (Roberts, 1987).

Pollution may be a contributing factor in bleaching events, and increased anthropogenic stress in the form of farm run-off, oil spills, and sewage discharge is advancing the eutrophication of reefs around the world (Brown, 1987). Mass bleachings, however, tend to affect those reefs most removed from the sources of such local stresses. Off Jamaica, mass bleachings struck in 1987, 1989, and again in 1990. These events were unlike other local bleachings or signs of reef deterioration in that no appreciable stress gradient leading toward an obvious source (such as a town or river) were detected. Mass bleachings severely stressed reefs on the north, east, and west coasts of Jamaica, but only slightly on the southern coast, site of the greatest levels of sediment, sewage, and pollution inputs from human activity (Goreau, 1992).

The evidence suggests that there is a more wide-spread and subtle culprit responsible for mass bleachings events.

d. Elevated Water Temperatures and Coral Bleaching

High temperature water has been suggested as the causative element in a number of studies focused on locally unexplainable mass bleaching events (Glynn, 1984; Glynn 1988; Goreau, 1992; Brown, 1987; Bunckley-Williams and Williams, 1988; Goreau et al., 1992; Brown and Suharsono, 1990; Glynn and D'Croz, 1990; Glynn and DeWeerdt, 1991; Lang et al., 1988; Yonge and Nichols, 1931). One example of such a case was the severely bleached reef system of the Galapagos Islands affected by the 1983 El Niño event. Coral mortality was observed to be nearly 97% and was attributed to elevated water temperatures (Glynn et al., 1988).

Researchers argue that corals live close to their maximum temperature threshold during the warmest summer months, and a slight increase over that threshold may stress the corals, leading to bleaching (Coles et al., 1976; Brown, 1987). The severe bleaching that hit the eastern tropical Pacific was found to correlate very closely with the El Niño related anomalous SST warming in the region (Glynn et al., 1988). Studies also found elevated SST patterns in the Caribbean corresponding to the mass bleaching events of 1987 (Goreau et al., 1992; Williams, 1988). The unprecedented nature of bleaching events in the 1980s have led some to claim global warming as the culprit (Bunckley-Williams and Williams, 1988). A climatologically significant temperature rise, however, has yet to be proven (Elms and Quayle, 1991;

Atwood *et al.*, 1992).

In addition to field observations of elevated SSTs coincident with mass
bleaching events, a number of controlled laboratory studies have shown elevated water
temperatures induce bleaching (Glynn and D'Croz, 1990; Jokiel and Coles, 1977;
Coles *et al.*, 1976; Coles and Jokiel, 1977; Gates *et al.*, 1992). Upper level thermal
tolerances, however, are determined by geographic location and the normal sea water
temperature range to which corals are accustomed. This geographic acclimatization
has been demonstrated in the laboratory and through field observations of coral
thermal tolerance, contradicting classical theory that fixed thermal tolerance was a
taxonomic characteristic (Coles *et al.*, 1976). Studies involving comparisons of
tropical and subtropical corals from Hawaii and Enewetak, Marshall Islands, showed
that corals are acclimated to the ambient temperature patterns of their geographic area.
Upper level thermal tolerances were found to be nearly 2°C higher in Enewetak corals,
corresponding to the 2-5°C higher mean monthly seawater temperatures compared to
the Hawaii coral environment (Coles *et al.*, 1976). Corals in the Arabian Sea are
tolerant of water temperatures exceeding 34°C in offshore areas and 36°C for inshore
reefs, demonstrative of the geographical acclimatization of reef organisms (Coles,
1988).

It has also been shown that coral metabolism is directly related to water
temperature; affecting growth, photosynthesis, and respiration. Study of growth
records and laboratory growth experiments have shown two calcification minima
normally occur annually, indicative of stress during the warmest and coldest times of

the year (Coles *et al.*, 1977; Oliver, 1985). Hawaiian corals exhibited optimal growth at the natural summer mean level (26.1°C) and minimum growth near 22°C, the ambient winter temperature. In controlled laboratory conditions, the same corals reduced calcification levels, bleached and eventually died from prolonged exposure to 30°C water (Jokiel and Coles, 1977). Experiments investigating the effect of water temperature on photosynthesis and respiration have also shown a direct linear relationship between reef coral metabolism and temperature. In these studies tropical corals from Enewetak Atoll were shown to maintain higher levels of primary productivity at elevated temperatures compared to Hawaiian corals. Once again showing the effects of acclimatization as well as the temperature domination of metabolism. For corals from both regions, continuous elevations in water temperature above ambient levels spurred increased respiration and photosynthesis. Respiration, however, increased at a greater rate, effectively reducing autotrophic capacity (Coles and Jokiel, 1977). Bleaching was the ultimate result of elevated temperature, induced either by a few days exposure to water 3-4°C above summer ambient levels, or longer exposure (several weeks) to temperatures 1-2°C over ambient summer temperatures (Jokiel and Coles, 1990).

Bleaching susceptibility appears to be correlated with respiration rate. High levels of incident light contribute to increased respiration levels and may accelerate bleaching at higher temperatures (Jokiel and Coles, 1990). The connection of bleaching susceptibility to respiration may explain the varying resistance of different coral species. Despite geographic acclimatization, taxonomic differences in

vulnerability to bleaching and related mortality exist at individual reef sites

(Buddemeier and Fautin, 1993). Jokiel and Coles (1974, 1977, 1990) posit that corals

with higher respiration rates (related to autotrophic output) are more susceptible to

bleaching. Perhaps it is the coral's inability to maintain normal production rates with

increasing respiratory demands that ultimately leads to the breakdown of the symbiotic

relationship with zooxanthallae (Coles and Jokiel, 1977). Branching corals have

higher metabolic rates, reflected in more rapid growth and recruitment levels, and are

also more susceptible to bleaching than other corals in the same environment

(Buddemeier and Fautin, 1993; Goreau, 1993).

Increased ultraviolet (UV) light has also been suggested as a possible causal

stress in bleaching events (Jokiel, 1980). Evidence of the role of light stress is seen in

partially affected colonies bleaching on their upper surfaces but maintaining normal

coloration on their sides and undersides (Glynn, 1983). Additionally, shallower depths

of reefs bleaching more severely may be evidence of the impact of UV-radiation

(Bunckley-Williams and Williams, 1988). UV penetration has been measured down to

25m on a Jamaican reef and was reported to be 20-25% of surface values at a depth of

10m (Fleischmann, 1989). Bleaching has been observed down to depths of 70m or

greater, beyond the greatest depth to which UV-radiation was measured in Jamaica,

therefore potentially increased UV-radiation alone cannot account for the full extent of

mass bleachings. Reef corals also contain UV absorbing compounds, the

concentration of which is normally an inverse function of depth (Dunlap, 1986).

Laboratory work, however, on UV-light as a bleaching stress has shown that increased

temperatures can cause a decrease in UV absorbing compounds (Lesser *et al.*, 1990). Other laboratory work has shown that greater light intensity increases respiration rate (Jokiel and Coles, 1990). Therefore, a distinct possibility exists that a synergistic or at least additive effect of high temperature water and UV-radiation could be the direct cause of some bleaching on reef flats. Such an interacting combination of stresses may also contribute to more severe bleaching in shallow water, and would support the correlation of respiration rate with coral bleaching susceptibility.

Numerous stresses have been identified in relation to coral bleaching events. Mass bleachings on the scale of the 1983 and 1987 events are not readily connected to the majority of these stresses due to their widespread nature, sudden onset, and multi-species impact. Due to this observation, sedimentation, salinity shock, disease, and pollution have been ruled out in these cases. Mass bleachings appear during the warmest times of the year, so low temperature stress is also ruled out as the cause of mass bleachings since 1979. The remaining stressors: elevated water temperature and UV-radiation, seem to have the greatest impact on mass bleaching occurrence and severity. UV-radiation appears to play a secondary role to water temperature in inducing bleaching, exacerbating the deleterious effects of elevated water temperature by increasing respiration rates and accelerating the bleaching process. Therefore, elevated water temperature stress appears to be the main causative factor in the occurrence of mass bleaching events.

Remote Sensing of Sea Surface Temperatures

NOAA has been generating operational satellite-derived multi-channel SST (MCSST) products since 1981. A polar-orbiting satellite circling the earth fourteen times per day at an approximate altitude of 850 kilometers covers each section of the oceans twice daily compositing swath widths of 2600 kilometers. The satellite uses measured brightness temperatures from three atmospheric windows (3.7, 11, and 12μm) in empirically derived algorithms (see equations 1 and 2 below) to obtain a value of actual sea surface temperature, T_s, in degrees Celsius (Robinson, 1985). The daytime algorithm uses two of the three channels, excluding the near-infrared (3.7μm) due to its proximity to the visible range, while the nighttime algorithm employs all three channels (Strong, 1992). MCSST algorithms are designed to remove the offsets of atmospheric water vapor and were developed through a comparison of satellite brightness temperatures (°K) with a series of nearly 100 drifting buoys (Robinson, 1985).

$$T_s = 3.0375 T_{11} - 2.0663 T_{12} - 264.79 \qquad \text{day (1)}$$

$$T_s = 0.9528 T_{3.7} + 0.99 T_{11} - 0.9528 T_{12} - 269.22 \quad \text{night(2)}$$

The presence of clouds can hamper the collection of satellite sea surface temperatures, so cloud removal techniques are important to quality-control the SST images. Daytime data can be screened utilizing the visible channels of the Advanced Very High Resolution Radiometer (AVHRR) to detect cloud/haze presence. Nighttime

cloud removal is a more complicated technique that compares SST values from three different algorithms: split (using the 11 and 12 µm channels), dual (using the 3.7 and 11µm channels), and triple (using all 3 channels) window. Cloud presence will cause the three different values to diverge, so if the algorithms do not agree, the cloud contaminated portion can be discarded. Gaps in the weekly data resulting from cloud contamination can then be eliminated by interpolation in data processing (Robinson, 1985).

A more severe and not so easily accommodated atmospheric influence is introduced by volcanic aerosol. Major volcanic eruptions such as *El Chichón* in 1982 and Mt. Pinatubo in 1991 can throw huge volumes of aerosols into the stratosphere over 25km high (Strong, 1984). Once above the tropopause, aerosols have a residence time on the scale of months to years in the lower layers of the stratosphere, away from major weather systems that would tend to wash them out. Small particles of sulfuric acid introduced into the stratosphere by a volcanic eruption attenuate the radiation from the earth, introducing a negative bias into the satellite derived SST values (see Fig. 4, p.29) when only algorithms designed to remove atmospheric water vapor are used (Strong, 1984). New algorithms have been developed which will hopefully remove the offset introduced by this problem (Strong, personal communication), but for current applications, the years 1982, 1983, 1991, and 1992 remain partially contaminated.

In this project, all statistical work with buoy comparisons, all mean MCSST values calculated, and comparisons between the temperature regimes of individual

years at reef sites use MCSST data from 1984-1990. Those years with volcanic contamination were discarded based on excessive offsets in the statistical analysis. A few analyses of early 1991 temperatures collected from before the eruption of Mt. Pinatubo (June 15) are included for bleaching years at some reef sites.

MCSST data were manipulated on the VAX workstations in the CPORS laboratory. Nighttime weekly average values at 0.2° lat/lon resolution were used to construct SST time series at buoy locations and reef sites. Nighttime data were used in lieu of daytime data because they demonstrated lower bias and greater accuracy when compared to *in-situ* ship-board measurements (Montgomery and Strong, 1994).

In this application of MCSST data to the coral bleaching problem, satellite grid-point time series were constructed for the four reef sites. The resolution limitations of the satellite (approximately 18km) would not allow direct sampling over coral sites. The forced extraction of the satellite temperatures from offshore locations avoided land contamination of the MCSST data. Any temperature threshold analyses employing this resolution of MCSST data will give temperatures only representative of those actually experienced by corals on a reef. A satellite-derived temperature threshold value for a specific reef site will tend to be lower than a threshold temperature measured on the reef site due to this limitation of the satellite data time series resolution. This expected offset is based primarily on observations of slightly warmer water temperatures at inshore versus offshore reef locations (Cook *et al.*, 1990).

Results

a. Comparison of MCSST to Moored-Buoy SSTs

Eleven individual buoy comparisons were conducted. Most buoy data were
retrieved through Internet from resources at NOAA's Pacific Marine Environmental
Laboratory in Seattle, Washington. The remaining data came from NOAA's National
Oceanographic Data Center in Washington, D.C. on CD-ROM. All buoy data came in
the form of individual day or hourly SST measurements. The daily values were
averaged to obtain weekly values to compare with the MCSST record. Hourly
measurements coincident with the satellite pass were retrieved and again averaged into
weekly values for comparison with the satellite using a Turbo Pascal program. Table
III below shows the statistical results of the comparisons, with buoy position and
length of record indicated. For this study's observation period from 1984 - 1990, the
average bias was less than 0.1°C and standard error of estimate 0.5°C.

| Buoy	Weeks	Std Err	Bias (°C)
25.9N, 89.7W	279	0.556	-0.042
26N, 93.5W	269	0.584	-0.087
23.4N, 162.3W	305	0.592	-0.087
2S, 110W	196	0.456	-0.087
2N, 110W	207	0.689	-0.439
8S, 110W	64	0.199	0.023
0S, 124W	143	0.435	-0.018
2N, 140W	184	0.474	-0.208
0S, 169W	110	0.367	0.097
2S, 165E	183	0.497	-0.002
2N, 165E	113	0.431	-0.005

Table III Statistical results from 11 MCSST/*in-situ* buoy comparisons.

These results are some of the best MCSST/*in-situ* comparison results obtained in the history of MCSST production (Strong, personal communication). Individual buoy versus MCSST comparisons are shown below (see Figs. 3, 4, 5, and 6). In some cases, the performance of a buoy was questioned where a poor correlation with the MCSST record was found. This was based on the good statistical comparison with an adjacent buoy (note an apparently good buoy at 2S, 110W, and its presumably defective neighbor at 2N, 110W in Table III). Another problem encountered in this comparative study was lost buoy data -- large gaps of time when the buoy sensor failed or the buoy was not transmitting (see figure 3).
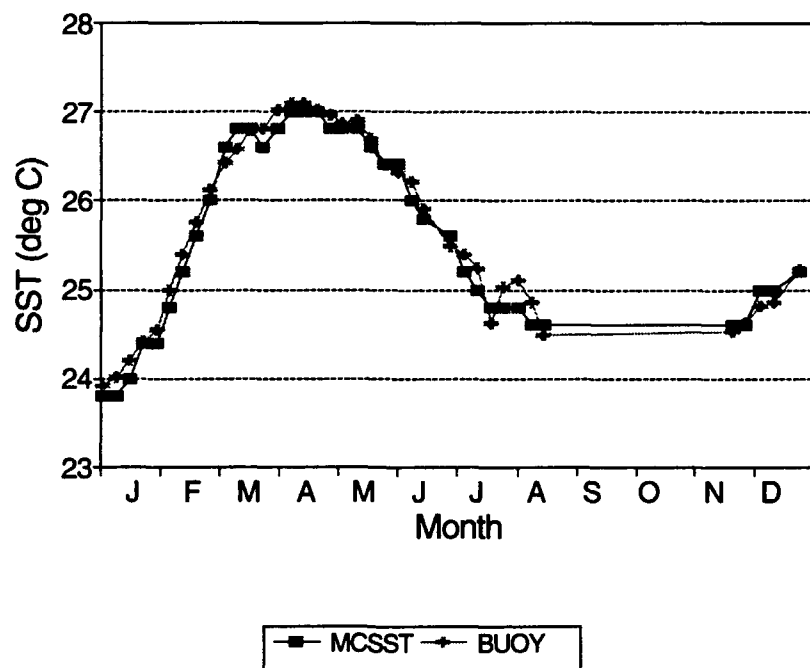
Figure 3 Buoy vs. MCSST comparison from 1986 at 8S, 110W. Note gap (August-November) due to lost buoy data.
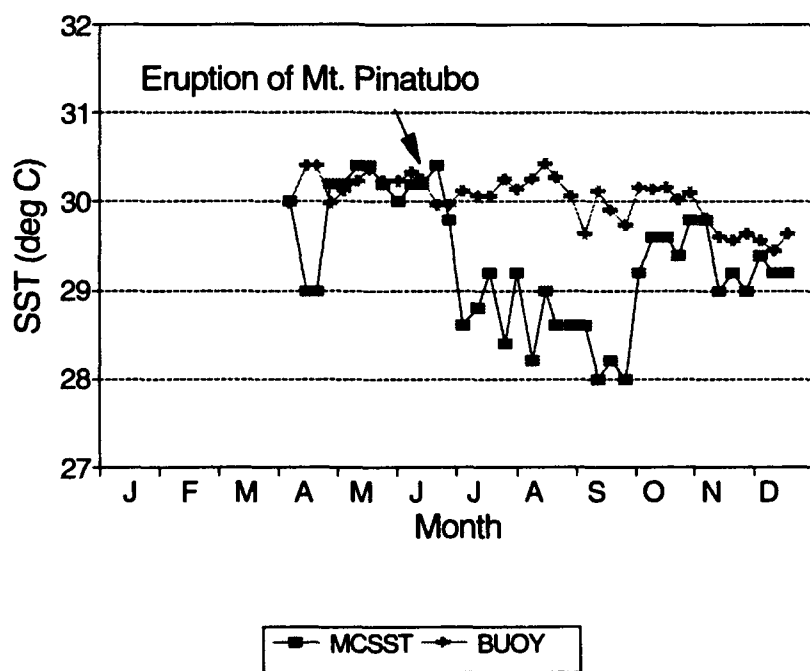
Figure 4 Buoy vs. MCSST comparison from 1991 at 2S, 165E. Note negative offset (June-October) in MCSST due to volcanic interference.
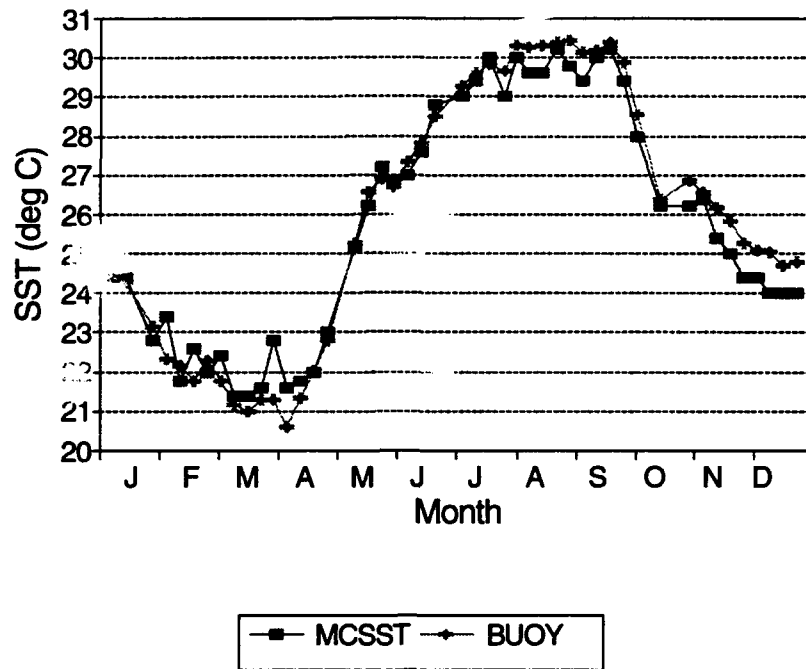
Figure 5 Buoy vs. MCSST comparison for 1987 at 25.9N, 89.7W (Gulf of Mexico).
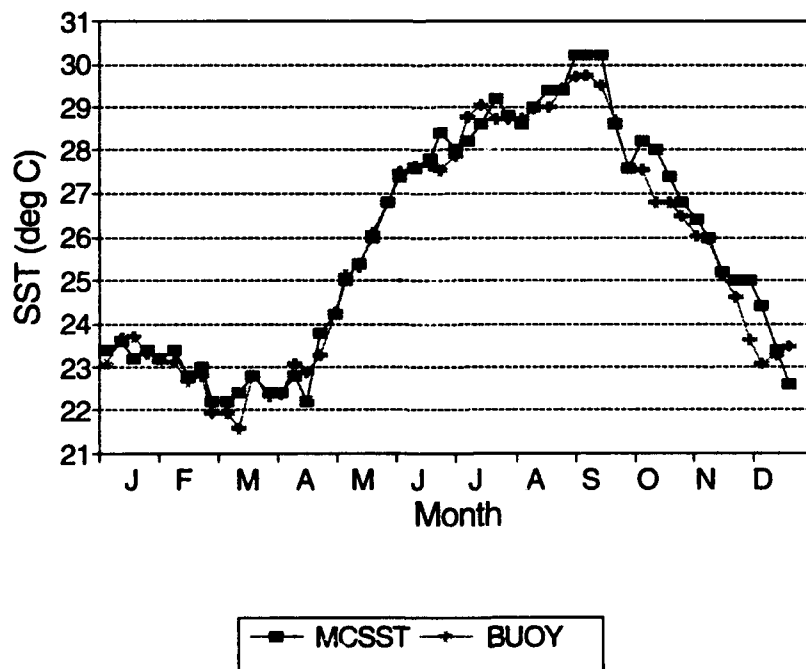
Figure 6 Buoy vs. MCSST comparison from 1989 at 26N, 93.5W (Gulf of Mexico).

**b. Reef Site Coral Bleaching Records and MCSST Analyses**

i. Bermuda

Coral reef bleaching related to remotely sensed SSTs at Bermuda was previously investigated by Montgomery and Strong (1994). Their work involved sea-truthing of both daytime and nighttime MCSST data against ship-collected *in-situ* measurements from the Bermuda Biological Station. Their results demonstrated a significantly lower bias in nighttime MCSST data and led to the exclusive use of nighttime imagery in this study. Reef bleaching at Bermuda related to SST patterns was examined to review the results of Montgomery and Strong (1994) and to expand on their analysis of the bleaching events.

Bleaching of zoanthids between May and July 1988 on shallow lagoonal reefs and rim margin reefs was the first indication of any sort of bleaching event at Bermuda that year. August and September reef transect studies and tow surveys revealed bleaching of several species of corals. Most severely bleached were specimens of *Millepora alcicornis* on outer rim reefs. *Montastrea annularis* and *Diploria labyrinthiformis* were two species also more severely bleached on outer reefs than on inshore reefs. Apparently, this event was the first of its kind to have been observed at Bermuda. It coincided with the highest sea surface temperatures (28.9-30.9°C inshore, 28-28.5°C offshore) recorded in 38 years (Cook *et al.*, 1990). Bleaching of similar scope and intensity was also reported during 1991 (Montgomery and Strong, 1994).

Montgomery and Strong (1994) developed the first satellite-derived temperature

threshold at Bermuda. They found bleaching corresponded to temperatures exceeding 28.1°C in the MCSST record. The analysis conducted in this study supported their threshold of 28.1°C. However, this temperature value alone does not incorporate the importance of duration of elevated water temperatures in inducing bleaching (Jokiel and Coles, 1990). A histogram of the satellite temperatures for the years 1987 through 1991 was conducted to look at the residence time of different water temperature ranges in the satellite record (see figure 8). Temperatures were divided into 0.5°C bins, with only the upper portion of the temperature range shown for Bermuda (the annual SST range at Bermuda exceeds 10°C--showing the full range would have unnecessarily complicated the display when only high end temperatures were of interest).

The derived satellite temperature threshold for Bermuda was 28.1°C (Montgomery and Strong, 1994). It can be seen by inspection of the MCSST plot for 1982-1992 that the years 1988 and 1991 show the highest temperatures for the record, each year exceeding 28.1°C (see figure 7). The three dimensional histogram display gives an even better indication of warming in those years as opposed to non-bleaching years. In both 1988 and 1991, four weeks averaged in the 28.0-28.5°C range, while such a strong presence of warm water is not seen in the non-bleaching years of 1987, 1989, or 1990 (see figure 8). This shows the relative strength of the heating stress in 1988 and 1991 was much greater than in non-bleaching years.
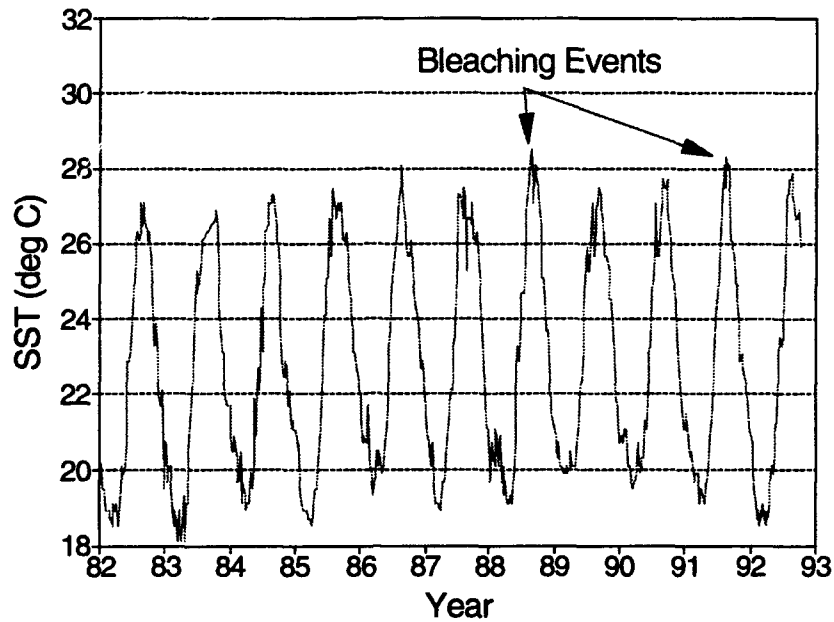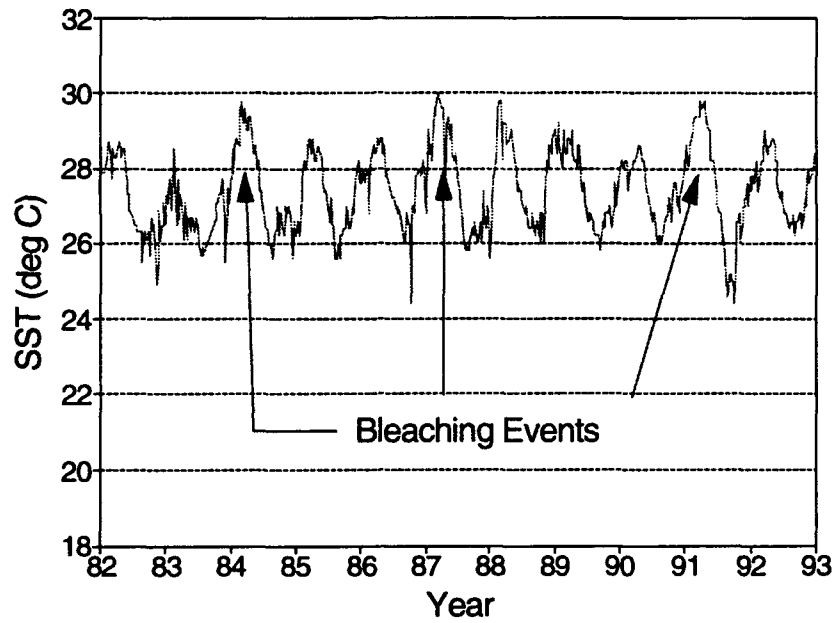
Figure 7 Bermuda MCSST from 1982-1992. Note higher SSTs and bleaching events in 1988 and 1991.
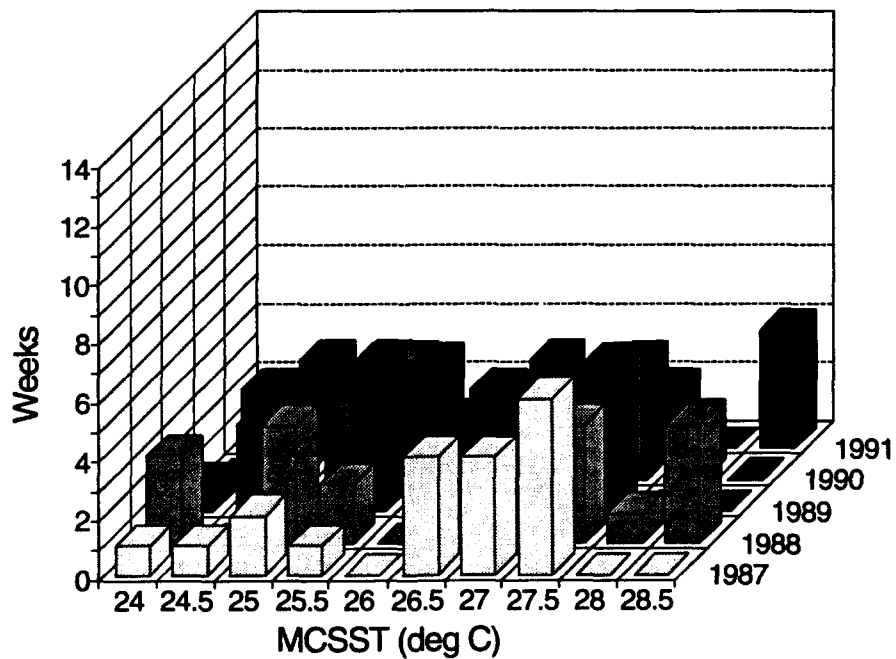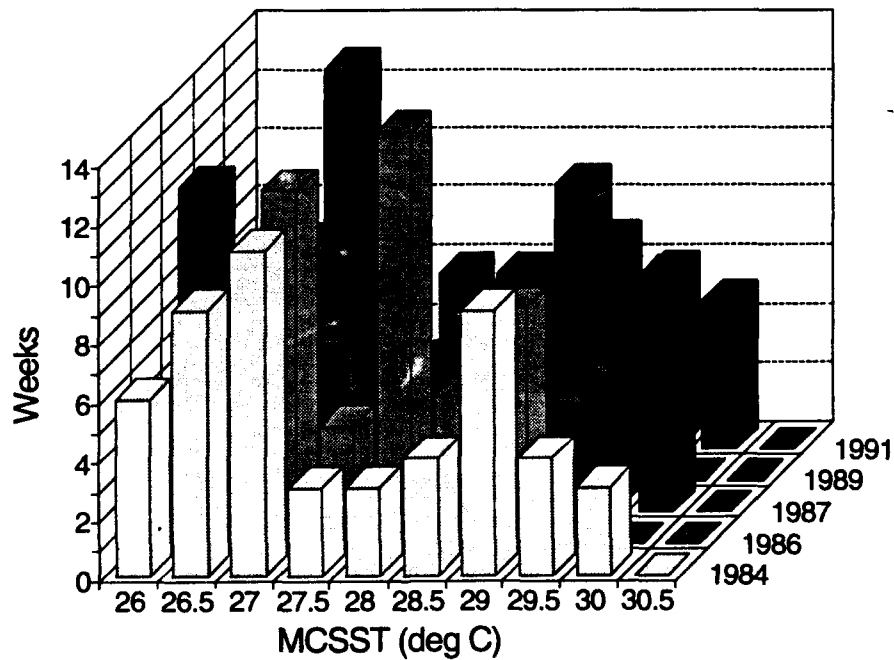

Figure 8 Three dimensional histogram display for 1987-1991 at Bermuda. MCSST values are divided into 0.5°C bins, the values on the x-axis represent the highest temperature in each bin. Bleaching in 1988 and 1991.

ii. Tahiti

The bleaching reports from Tahiti are less complete than from the other sites at Bermuda and Jamaica. Mass bleachings, however, have taken place on the reefs off Moorea Island in 1984, 1987, and 1991 (T.J. Goreau, B. Salvat, personal communication). Inspection of the MCSST record from 1982-1992 indicates those three years were the warmest in terms of peak temperatures (see Fig. 9). A satellite-derived threshold temperature of 29.8°C was generated from a comparison of bleaching and non-bleaching years at Tahiti. A histogram analysis was conducted at this site for the years 1984, 1986, 1987, 1989, and 1991 (see Fig. 10). Stronger presence of warm water is noted for the bleaching years of 1984, 1987, and 1991, with 2, 7, and 5 weeks of water temperature in the 29.5-30°C range respectively. Here again there is evidence connecting elevated water temperature to mass bleaching events.

Figure 9 Tahiti MCSST from 1982-1992. Note higher SSTs and bleaching events in 1984, 1987, and 1991.

Figure 10 3-dimensional histogram display of MCSSTs from 1984-1991 at Tahiti. MCSST values are divided into 0.5°C bins, x-axis values represent the highest temperature in each bin. Bleaching in 1984, 1987, and 1991.

iii. Jamaica

The reefs of Jamaica have been closely observed for over 40 years by Thomas J. Goreau and the late Thomas F. Goreau (1992). Their work may make the reefs of Jamaica some of the most thoroughly studied in the world. A general deterioration of the Jamaican reef system has been observed since the beginning of the observation period in 1951. Mass coral bleaching events, however, unlike other stresses contributing to reef degeneration, had not been observed for the first 34 years (1951-1986) of study in Jamaica (Goreau, 1992).

Mass coral reef bleaching events that affected many of the Jamaican reefs were observed in 1987, 1989, and 1990 (Goreau et al., 1992). The north, east, and west coasts of Jamaica were most severely affected, in contrast to the south coast where most of the sediment, sewage, and pollution problems persist (Goreau, 1992; Goreau and Hayes, 1994). The MCSST retrieval site was therefore chosen off the north coast of the island. A number of other works have shown elevated water temperature presence during the mass bleaching events of 1987, 1989, and 1990 (Goreau and Hayes, 1994; Goreau et al., 1992). Goreau has suggested a temperature threshold of 30°C over which bleaching is observed (Goreau et al., 1992). Inspection of the MCSST time series for Jamaica reveals mass bleaching years were significantly warmer than non-bleaching years (see figure 11). A satellite temperature threshold for Jamaica was selected at 29.6°C. Each event followed a slightly different schedule and pattern of bleaching. Goreau noted a small rise in SST values of long duration took place in 1987, while shorter periods of more intense temperatures seemed to be

responsible for the bleachings in 1989 and 1990. The severity of the events increased from 1987 to 1989 with 1990 being the most intense bleaching year, corresponding to the measured SST elevations (Goreau *et al.*, 1992). The histogram analysis of the MCSST patterns from 1986-1990 supports this observation (see figure 12). Three weeks of water temperatures in the 29.5-30°C range were recorded by the NOAA satellite for 1987. 1989 witnessed an even greater level of heating, with 7 weeks in the 29.5-30°C range and 1 week of water of 30-30.5°C. The temperatures in 1990 were as high as 1989, but were sustained for an even greater period of time. Six weeks of water between 29.5 and 30°C and 3 weeks between 30 and 30.5°C were recorded for 1990, corresponding to the year of most intense bleaching for Jamaica.
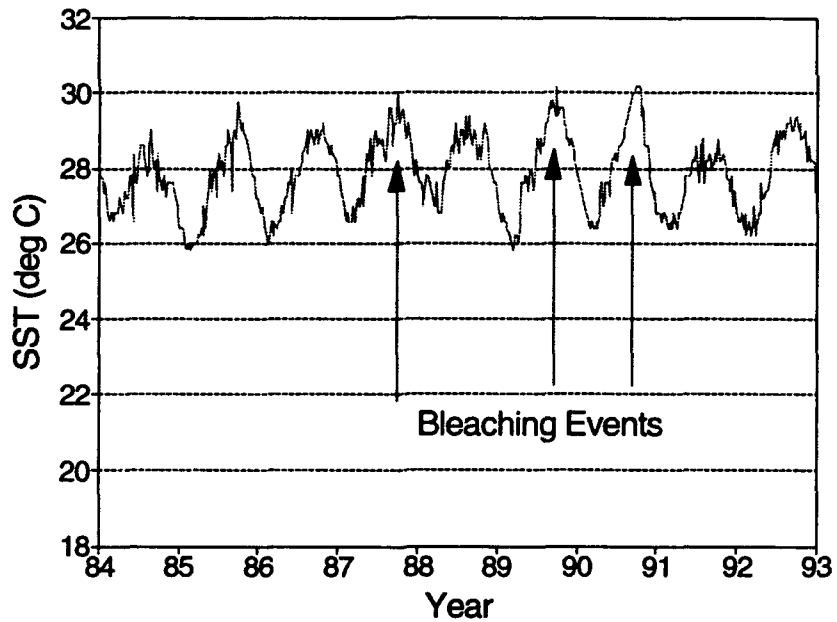
**Figure 11** Jamaica MCSST from 1984-1992. Note higher SSTs and bleaching events in 1988 and 1991.
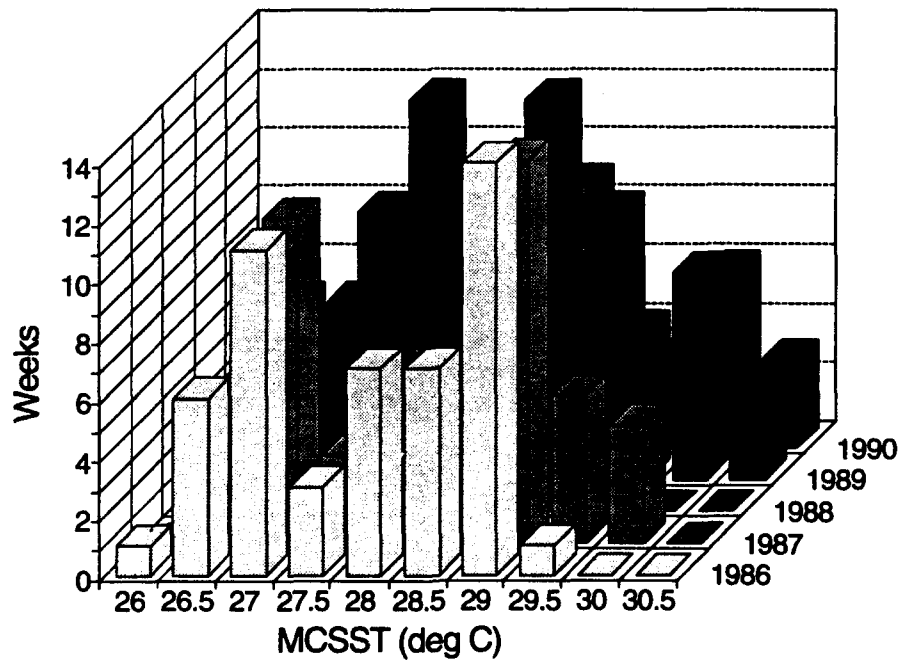
Figure 12 3-dimensional histogram display of MCSSTs from 1986-1990 at Jamaica. MCSST values are divided into 0.5°C bins, the values on the x-axis represent the highest temperature in each bin. Bleaching in 1987, 1989, 1990.
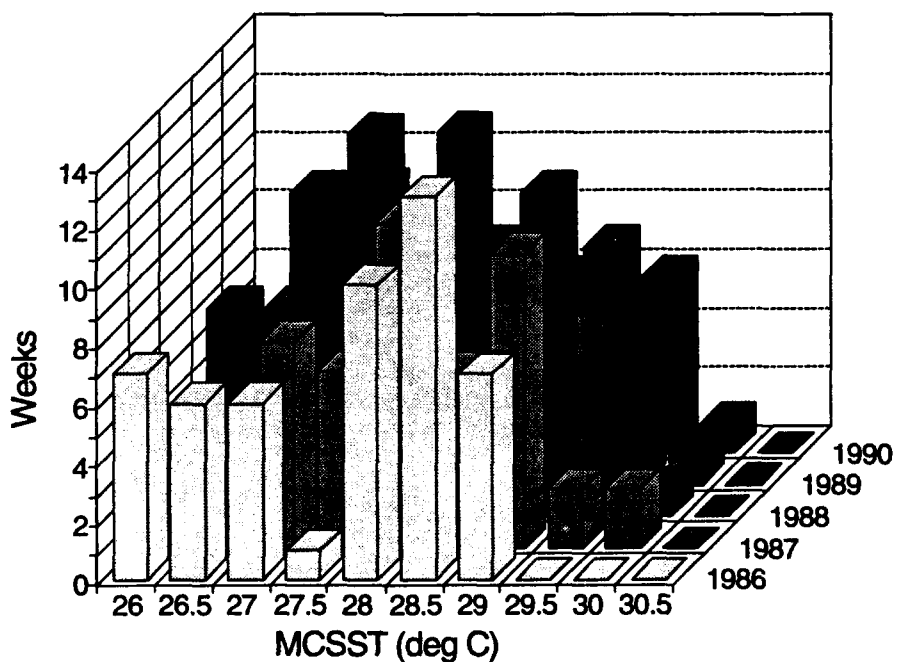
iv. Belize

According to Glynn (1993) only two of the highly studied reef systems have not reported mass bleaching events. This includes the barrier reef system in Belize and reefs in the Gulf of Eliat in the Red Sea. Belize was selected as a control site for this reason, and the MCSST record for this site was studied in conjunction with the MCSST trends at Jamaica. The MCSST mean temperature at Belize was 27.7°C, very close to the MCSST mean at Jamaica of 27.8°C. The latitudinal difference in position between the two sites is only 2° (see Table II), and both sites have a similar ambient temperature range. Therefore, using Belize as a control site for comparison to Jamaica should be appropriate.

The MCSST record at Belize does not show any appreciably higher peaks in SST for any individual years (see Fig. 13). 1987 appears to be generally warmer than other years in the record, but there was not any bleaching reported for Belize during that year (the year of the major Caribbean bleaching event). A histogram analysis of the yearly temperatures at Belize from 1986-1990 shows 1987 to be slightly warmer than other years, with 2 weeks of SSTs in the 29.5-30°C range (see Fig. 14). This is contrasted with the 5 weeks of SSTs in the same zone for Jamaica that year. The 1989 and 1990 records from Belize both had strong presence of 29-29.5°C water (5 and 6 weeks respectively), but only 1 week each of water temperatures in the 29.5-30°C range. Temperatures in Jamaica were much stronger for the same years (see previous discussion). Inspection of the multi-year three-dimensional histogram plots from both sites reveals that Jamaica experienced significantly higher temperatures

during bleaching years with same-year milder temperatures at the Belize site

coincident with non-bleached reefs.
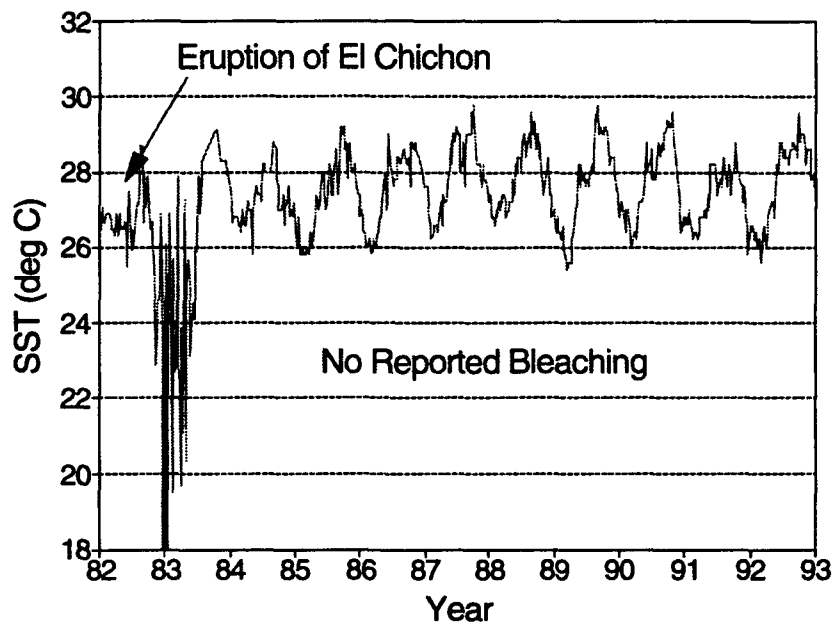
Figure 13 Belize MCSST from 1982-1992. Bleaching was not observed. Note noise in MCSST record following volcanic event.

Figure 14 3-dimensional histogram display of MCSSTs from 1986-1990 at Belize. MCSST values are divided into 0.5°C bins, the values on the x-axis represent the highest temperature in each bin. No reported bleaching.

c. Development of a Bleaching Index for Belize and Jamaica

Use of the histogram analysis gave an improved view of the connection

between elevated temperature duration and coral reef bleaching events. In an effort to

represent the relative heating stress a coral reef experiences in the course of one year,

a *Degree Heating Weeks* (DHW) index was developed. The index was based on a

mean MCSST value for each reef site. The mean MCSST was subtracted from each

weekly MCSST value for the entire uncontaminated record from 1984-1990.

Differences from the last 30 weeks of each year (corresponding to the warmest time of

the year and hence positive difference values) were summed to obtain the index value

(see Fig. 15). The resulting number was assigned the dimensions of Degree Heating

Weeks (DHW). This DHW value is representative of the cumulative heating stress on

the coral reef for a given year.

Plots of the DHW values from 1984-1990 for Jamaica and Belize reveal higher

heating stress values in 1987, 1989, and 1990 for both sites (see Figs. 16 and 17).

Belize experienced a high of 25 degree heating weeks in 1987, compared to 27 at

Jamaica for the same year. In 1989, Jamaica again had a higher DHW value of 31,

compared to the 24 observed at Belize. The final bleaching year at Jamaica during

this period was 1990 when we find the calculated DHW total to be 29, compared to

23 at Belize. When comparing these sites, we see that for each bleaching year at

Jamaica, the DHW value exceeded 26, while the non-bleached reefs off Belize never

experienced over 25 degree heating weeks. It is proposed that a heating stress of 26

DHW may indeed be the threshold tolerance of coral reefs at these two locations.
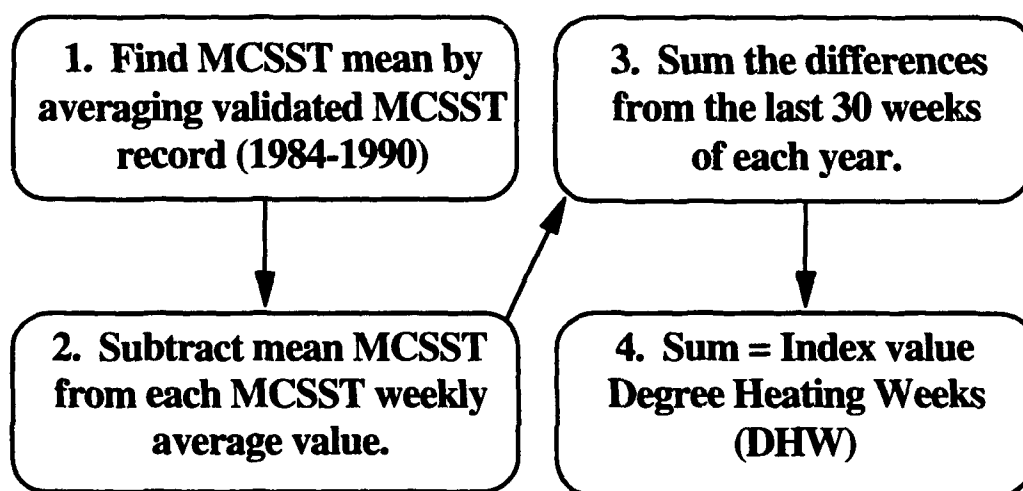
Each index plot also shows a breakdown of the relative contributions from the high temperature ranges (see Figs. 16 and 17). This breakdown partially reflects what was shown in the histogram analyses, giving an indication of peak temperature presence on the reef. Most importantly, the portion of each index value from SSTs exceeding 30°C (red) should be noted. The total index value gives an indication of overall heating stress, and the breakdown of the DHW totals as shown in figures 16 and 17 can give an intimation of the relative strength of peak temperatures from each year.

The DHW index, however, does not account for other potentially important characteristics of the temporal pattern of SST changes and coral bleaching events. The rate of temperature change (*i.e.*, thermal shock) may play a very significant role in the stress response of reef organisms, and should be considered in future research. Additionally, this index fails to distinguish between consecutive and non-consecutive heating weeks. Inspection of the 1987 MCSST record for Jamaica shows two periods of temperatures above 29.5°C interrupted by one week of 29.2°C SST (see Fig. 18). Had the 5 weeks of 29.5-30°C SST water been sequential, we would expect a stronger bleaching response. Finally, the index does not consider any carry-over effects from previous bleaching years. Full reef recovery can take several months to a year, therefore successive annual events would more dramatic than isolated ones. An example where this should be considered is for the 1990 bleaching at Jamaica which followed a strong event from the previous year. The three-dimensional histogram plots and MCSST records for 1989 and 1990 (see Figs. 16, 17, and 19, 20) indicate

the greater duration and sequential nature of SSTs measured in the 30-30.5°C range in 1990. The index value for Jamaica was 29 for 1990, compared to a DHW value of 31 for 1989, yet the bleaching was reported as more severe for 1990 (T. Goreau, personal communication). This can also be seen in the index breakdown in figure 17; the strength of SSTs in the 30-30.5°C range in 1990 was much greater than comparable temperatures from 1989. This example shows the importance of thermal shock considerations, sequential versus non-sequential heating weeks, and peak temperature presence as well as the carry-over effect from preceding strong events. Despite these shortcomings, the DHW index can still be an effective gauge of overall heat stress relative to the mean MCSST temperature on a reef, as well as a predictor of bleaching events. This index shows potential for expansion in future research.

Bleaching Index Procedure

for Jamaica and Belize

1. **Find MCSST mean by averaging validated MCSST record (1984-1990)**

3. **Sum the differences from the last 30 weeks of each year.**

2. **Subtract mean MCSST from each MCSST weekly average value.**

4. **Sum = Index value Degree Heating Weeks (DHW)**

**Figure 15** Procedure for calculating Degree Heating Weeks index values.
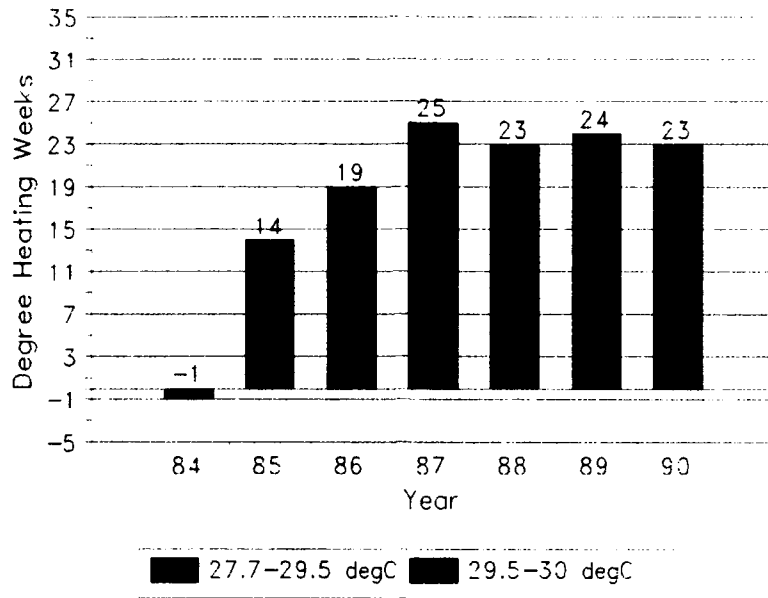
Figure 16 Degree Heating Weeks index values from 1984-1990 for Belize with the relative contributions of 27.7-29.5C and 29.5-30C SST shown.
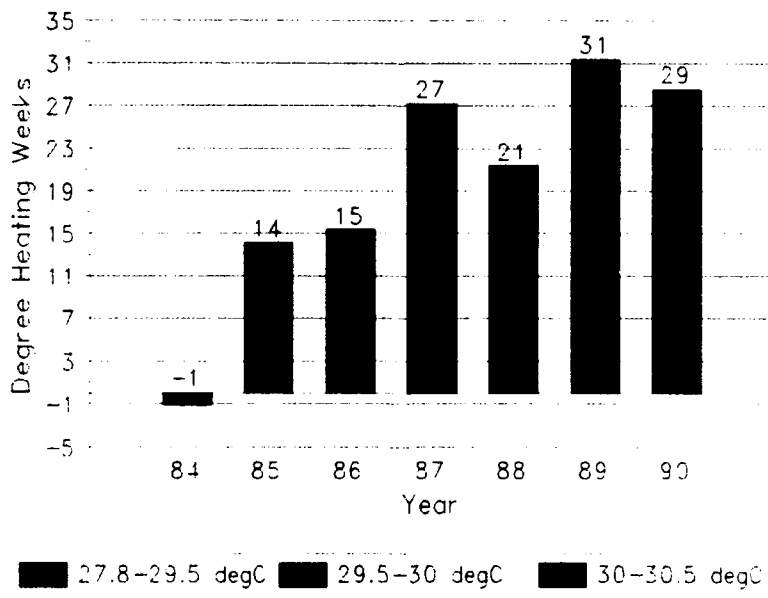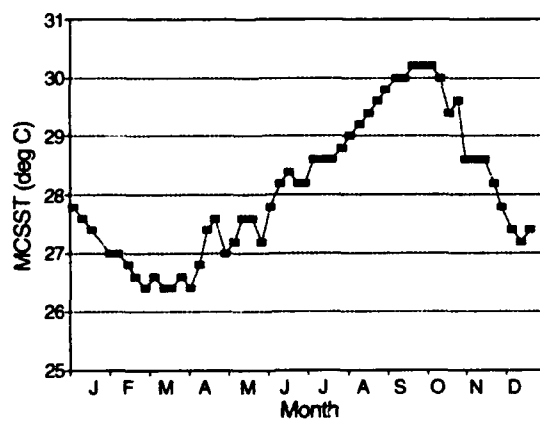

Figure 17 Degree Heating Weeks index values from 1984-1990 for Jamaica. Relative contributions of 27.8-29.5C, 29.5-30C, and 30-30.5C SSTs shown.
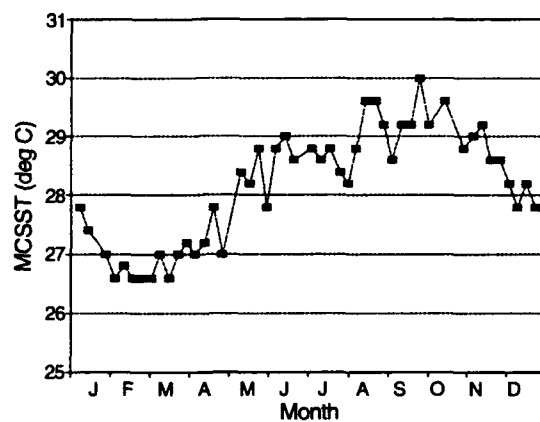
Figure 18 MCSST record from 1987 for Jamaica.
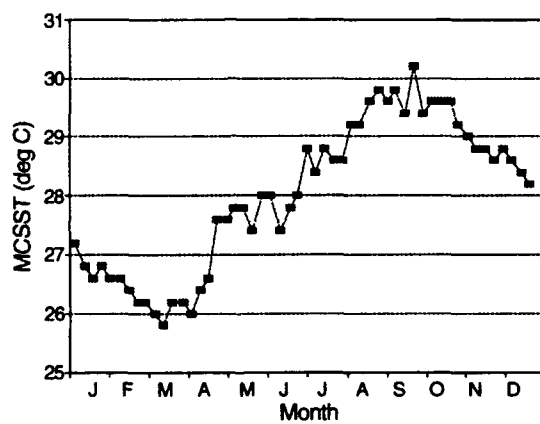
Figure 19 MCSST record from 1989 for Jamaica.

Figure 20 MCSST record from 1990 for Jamaica

Conclusions

This study shows that major coral reef bleaching events since 1979 were unexplainable in terms of previously recognized local bleaching stressors. Evidence strongly suggests elevated water temperature as the primary factor in many cases of mass bleaching. The problem of making the connection between high water temperature and mass bleaching events is primarily a lack of quality *in-situ* SST time series at virtually all of the bleached reef sites. Weekly averages of nighttime NOAA MCSST data (1982-1992) were used to investigate the role of elevated SSTs in coral bleaching events. Results indicate that not only the intensity, but also the duration of elevated water temperature on a reef, can be an excellent predictor of the strength of a coral bleaching event. The three repeatedly bleached sites this study examined included Bermuda, Jamaica, and Tahiti. The control site at Belize was a well studied reef that had not experienced bleaching for the period of observation (1984-1990).

MCSST data were validated for periods not contaminated by volcanic aerosols. Sea-truthing of satellite data was accomplished by comparing MCSST weekly averages to in-situ SST measurements made by NOAA moored-buoys. The comparative study flagged the years 1982, 1983, 1991, and 1992 as contaminated by volcanic aerosols. Consequently, only MCSST data from 1984-1990 was analyzed in relation to coral bleaching events excepting some early 1991 temperatures recorded before the eruption of Mt. Pinatubo (June 15, 1991).

Satellite temperature "thresholds" were derived from the original comparison of the MCSST time series with the coral bleaching record at each site. Analysis of the

MCSST record revealed higher water temperatures during bleaching years when compared to non-bleaching years at all sites. In order to investigate the effect of elevated SST duration on the occurrence and severity of bleaching events, histogram analyses of temperatures during bleaching and non-bleaching years were conducted at the four study sites. Longer periods of elevated water temperatures were seen at all reef sites during years with bleaching. Finally, the idea of coupling elevated SSTs and their residence times led to the development of a heat stress index for the Belizean and Jamaican reefs, based on the validated MCSST records. These sites were selected for the index due to their close latitudinal proximity, comparable ambient temperature range and similar MCSST (1984-1990) mean temperatures (Belize MCSST mean = 27.66°C, Jamaica MCSST mean = 27.8°C). A *Degree Heating Weeks* (DHW) index was developed in order to represent the level of heating stress experienced by a reef in a given year relative to other years within the observation time period of 1984-1990. A value of greater than 26 DHW is proposed as the threshold accumulated heat tolerance for the Jamaican and Belizean sites based on a comparison of the index values from both bleaching and non-bleaching years. It remains to be seen whether this same hypothesis works equally well for other reef sites at comparable latitudes with similar mean SSTs.

In each analysis technique: MCSST record inspection, histogram analysis, and degree heating weeks calculations, higher water temperatures and increased levels of heating coincided with all reported coral reef bleaching events.

Discussion

This research has shown that elevated water temperatures have often accompanied mass coral bleaching events, particularly over the past 14 years. Furthermore, the relative intensity and duration of high water temperature seems to dictate the strength of the bleaching response. The influence of a number of other interacting stresses needs to be investigated in conjunction with future research designed to study the intricacies of the coral bleaching/elevated water temperature relationship.

Mass bleaching events that took place in the 1980s and early 1990s were truly unprecedented. A number of sources have suggested global warming may be potentially responsible for the increasing frequency and world-wide spread of coral bleaching throughout the tropics (Bunckley-Williams and Williams, 1988; Glynn, 1993; Brown, 1987; Bunckley-Williams and Williams, 1990), while others refute such claims (Elms and Quayle, 1992; Atwood et al., 1992). Proponents of the global warming scenario argue that the world's reef systems are acting as sensitive ecological alarms, warning of eminent and potentially rapid temperature change that could destroy coral reefs all together. Past climate fluctuations, equally as large as predicted greenhouse-forced global temperature change (Firor, 1990), were more gradual transitions that took, on average, an order of magnitude longer to complete (1000 vs. 100 years). The ability of coral reef ecosystems to respond to rapid climate change on the same time scale of coral lifetimes and community turnover is untested and unknown (Smith and Buddemeier, 1992).

New reports of mass bleaching underway off Tahiti and in the islands of French Polynesia, as this paper is written (April 1994), indicate the problem has not gone away (B. Salvat, personal communication). Whether mass bleaching events are the result of normal climate fluctuations or changes accelerated by mankind remains to be discovered, but if current trends in the frequency and spread of bleaching events continue, the world's reef ecosystems will be severely threatened. The connection between strong warming events and damaging coral bleaching has been demonstrated in this study, but a tremendous amount of research on more specific aspects of reef bleaching events, reef ecology and climate change is still required before one can truly understand the consequences of bleaching and potential global change on coral reef ecosystems.

Acknowledgments

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