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# THE WORLD-WIDE CORAL REEF BLEACHING CYCLE AND RELATED SOURCES OF CORAL MORTALITY

BY

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## ABSTRACT

World-wide "coral reef bleaching complexes" occurred in 1979-80, 1982-83 and 1986-88. Each included a "preceding event" 1 year (1979, 1982, 1986) before the most extensive ("main event") bleaching began. The 1986-88 complex also possessed a "following event" (1988). A number of minor bouts also occurred during each complex. Preceding events may be used to predict main bleaching events. We believe the world-wide coral reef bleaching complex "cycle" is caused by increased global temperatures of the 1980's. The progressive deterioration of inshore regions, including coral reefs, may have contributed to the intensity of the events. El Niño southern oscillation (ENSO) events of 1982-83 and 1986-88, on top of these problems, increased overall seawater temperatures, or provided conditions favoring increased inshore temperatures, to the levels necessary to bleach and kill coral reef photosymbiotic hosts. Decreased temperatures also caused minor bouts in 1988, 1989 and possibly other times. Deterioration of coral reefs has also lowered photosymbiotic hosts' resilience, or resistence to the bleaching process. Our model explaining coral reef bleaching employs increased global temperatures, increasing deterioration of reefs, and ENSO events. These conditions are not only well established, but seem almost certain to continue. The cycle may repeat in 1991 or 1992, possibly with more intensity, and will probably continue and increase until coral dominated reefs no longer exist.

## INTRODUCTION

Coral reef bleaching has recently attracted considerable interest when spectacular and sudden bleaching occurred in 1987. This event led to a U. S. Senate Hearing (Hollings, 1988); Special Bleaching Sessions during scientific meetings in Mayaguez, Puerto Rico (November 1987), Curacao (November 1987), Sarasota, Florida (May 1988), Florida Keys (June 1988), San Salvador, Bahamas (June 1988), Townsville, Australia (August 1988), La Parguera, Puerto Rico (May 1989), and Havana, Cuba (June 1990); and a recent special volume by Brown (1989). In this paper, we describe the bleaching events of 1987-1988, a few previous bleaching occurrences which have not been published, and relate them to previously published reports of other bleaching events. We feel these events fall into patterns of world-wide bleaching complexes and further form a continuing cycle of bleaching. Our data set for 1986-1988 allows us to correlate conditions with events and bouts, to suggest a cause for the recent events, and, in combination with published accounts, to suggest an overall cause for the cycle. The escalation of deteriorating effects and signs of decline suggest an eventual loss of the coral reef system. A number of other major marine ecological disturbances require examination for common or related causes. The methods employed in our study and a proposed Alert and Communication Network are suggested as a practical means to follow these important, large-scale events.

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## MATERIALS AND METHODS

We issued more than 1,000 copies of 2 summaries and 3 questionnaires (sample copy in Appendix 1) and wrote 694 individual letters. We received 271 reports from 159 people in 48 countries (as of 3 June 1989). Records were recorded as case reports of the Caribbean Aquatic Animal Health Project. We took information from scientists at face value. Reports by amateur scientists, who tended to be too cautious in their estimates and descriptions, have generally been corroborated by coral reef specialists in the same or similar regions. The original data from these letters and completed questionnaires (personal communications) forms the major part of this paper. Much of the cited material comes from recent unpublished reports, abstracts, newsletter articles and proceedings. To save space, the names, addresses and/or affiliations of people who provided information are listed in the Personal Communications (PC) section found after the References. Last names cited in the text, tables and figures with the term "PC" refer to this list. Second last names are abbreviated in the text, but spelled out in the Literature Cited or PC listing when known. For convenience in this paper the abreviation "sp." following a genus name will indicate 1 unidentified species in the genus and the term "spp." 2 or more unidentified species. This does not suggest that this usage is generally correct. The term "host" is used instead of "photosymbiotic host" to save space. Reference to species of cnidarians and sponges in this paper refer to colonies of each host. The terms "colony of" or "colonies of" have been ommitted in most cases to save space. Use of animal species names to designate these complex photosymbiotic associations is merely for convenience, not an attempt to ignore the nature of these relationships. Specimens deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, are designated with USNM numbers. A list of all species (in taxonomic order) used in this paper and their authors is included in Appendix 2. The description of the 1987-88 events are presented largely in tabular form to make this data more easy to follow (Tables 1-22).

## DEFINITION OF TERMS

Many "bleaching" terms have been used in the past without adequate definition. We also employ some new combinations and new terms in this paper. For the purpose of clarity, the following definitions are provided:

**BLACK BAND DISEASE (BBD):** A cyanobacteria, *Phormidium corallyticum*, which invades Atlantic photosymbiotic hosts, possibly at points of damage, and inevitably destroys the entire colony. Disease progresses over stony coral heads in a circular pattern. The distinctive, narrow band of dark *P. corallyticum* filaments borders the remaining live coral leaving the white, bare skeleton in the center of the circle. Algae soon colonizes the bare skeleton (Ruetzler and Santavy, 1983; Peters, 1984). Ruetzler (1988) suggests that this pathogen may be a former cyanobacterial photosymbiont gone awry, similar to one he is studying in sponges. BBD or a similar condition also occurs in Indo-Pacific photosymbiotic hosts (Antonius, 1985). BBD has replaced "black line disease" as a term for this condition.

**BLEACHING:** Loss of photosymbiotic microorganisms (dinoflagellates, red and green algae, or cyanobacteria), or the pigments of these photosymbionts, or some of both, from tissues of host cnidarians, sponges, mollusks or other photosymbiotic host animals. The name comes from the whitening of many hosts which possess few pigments of their own. It replaces "blanching" (Jaap, 1985), "whitening" (Guillaume et al., 1983), etc. It should be accepted as a term and not placed in quotation marks.

**CORAL(S):** A common name for many anthozoans [octocorals (blue corals, soft corals, gorgonians), stony corals (also called "hard corals" or "true corals"), black corals] and hydrozoans (fire corals, stylaster corals). Often used incorrectly as a common name in place of stony corals or "hermatypic corals" (=stony, colonial, zooxanthellate photosymbiotic corals, with large skeletons, which form much of the living surfaces of coral reefs and the breakdown of their skeletal material provides much of the components for reef building).

**CORAL REEF BLEACHING:** A term suggested in place of "coral bleaching" because this condition is seldom limited to corals and most affected photosymbiotic hosts reside on coral reefs.

**DIE-OFF:** Death of more than 3, but fewer than 1000 individuals of animals or plants related in time, geographic area, and cause.

**EPIZOOTIC:** A disease temporarily prevalent among many animals of the same species. "Epidemic" applies only to humans, and should not be used to describe bleaching (Jaap, 1985) or diseases of corals (Williams and Williams, 1987).

**MAJOR MARINE ECOLOGICAL DISTURBANCE:** Mass mortality, epizootic or outbreak of organisms or conditions detrimental to biota affecting more than a few $km^2$ of area and occurring over more than a few days. Includes toxic red tides, fish kills, ciguatera outbreaks; but does not include direct effect of oil, toxic chemical, or radiation spills and/or contamination.

**MASS MORTALITY:** Death of 1000 or more individuals of animals or plants related in time, geographic area, and cause. Not interchangeable with "major marine ecological disturbance" or "epizootic".

**PHOTOSYMBIOSIS:** Photosynthetic mutualism between PHOTOSYMBIONTS (PHOTOSYMBIOTIC MICROORGANISMS) and PHOTOSYMBIOTIC HOSTS (see Bleaching definition). "Symbiont" was used incorrectly by Williams and Bunkley-W. (1989) as a term for both hosts and photosymbionts.

**UNITS OF BLEACHING (Figure 1):**

**BOUT:** The smallest portion of a bleaching disturbance which can be identified and separated in time.

**EVENT:** Made up of 1 or more bouts. An event is a period of continuous bleaching from the initial "outbreak" through final "recovery". Disturbances may vary slightly in time in different geographic locations and still be considered portions of the same event.

**BLEACHING COMPLEX:** A series of time-related bleaching events. Thus far, 2-3 events have made up a complex. Events in a complex may be recognized as "preceding", "main", and "following".

**BLEACHING COMPLEX CYCLE:** A complete round of bleaching, starting mid-way between complexes, through a complex and ending mid-way toward the next complex. Thus far, 1-2 years have separated complexes.

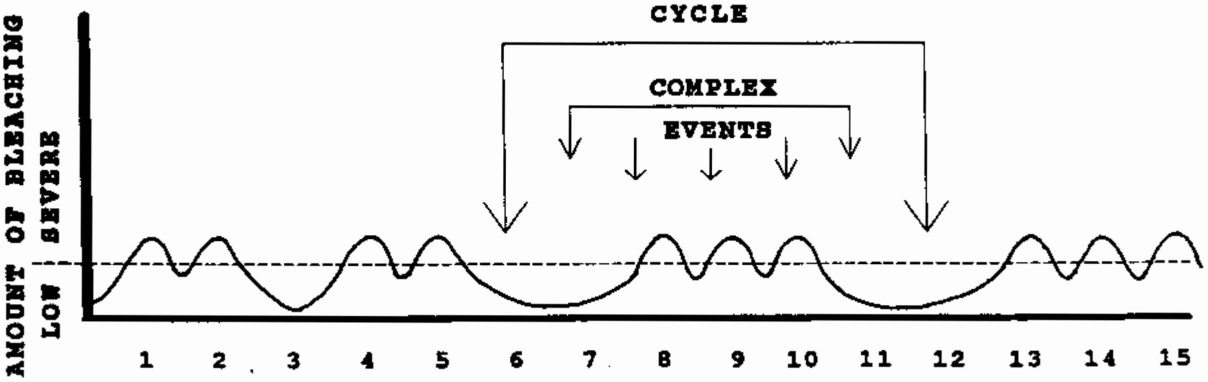


FIGURE 1. Diagrammatic Depiction of the Units of Bleaching.

**WHITE BAND DISEASE (WBD):** A disease of unconfirmed etiology, possibly due to adverse environmental conditions, with or without secondary bacterial infections, and/or due to a bacterial primary pathogen. WBD is characterized by sloughing of tissue starting from the base of the branches and progressing to the tips. Diseased corals may appear slightly lighter in color than normal. The disease may cease in some cases before an entire colony is destroyed. WBD or closely related conditions occur circumtropically in acroporids and other photosymbiotic hosts. The drastic decline of *Acropora* spp. in the tropical and subtropical Atlantic may be due to WBD, but almost all of these deaths have occurred in the absence of detailed examinations (Peters, 1984; Peters PC). WBD has replaced "white line disease" as a term for this condition. This disease and the related epizootics are in urgent need of definitive study.

**ZOOXANTHELLAE:** A common name for photosymbiotic dinoflagellates occurring in various marine hosts. Derived from names once proposed for generic taxa (Blank and Trench, 1986). Sometimes applied to photosymbionts other than dinoflagellates (loc. cit.), but we discourage such usage.

## DESCRIPTION OF THE 1987-88 EVENTS

### BEGINNING OF THE EVENT

Reports of mass loss of zooxanthellae from Florida, Mona Island, and Puerto Rico were noted by Williams and Bunkley-W. (1989). No similar reports were received from the Indo-Pacific or other parts of the Atlantic. The turbidity due to zooxanthellae in the otherwise clear waters of Puerto Rico and Mona Island indicated a relatively sudden and coordinated event. Reefs on the insular shelf edge (6.4 km offshore) and inshore reefs were intensely affected on the same day in Puerto Rico (Cintron PC).

A great variety in the speed of development of bleaching in different locations, different habitats and even at different times in the greater Caribbean area in 1987-88 was suggested by Williams and Bunkley-W. (1989) (Figs. 2,3). Since that paper, a report that bleaching developed suddenly in the Turks and Caicos (Lott PC) agrees with the original assessment of bleaching in that location by Spotte in Williams and Bunkley-W. (1989). In a closely monitored mangrove area in southwestern Puerto Rico, bleaching began suddenly in 1988 (and in 1986) (Perez-T. PC). In the Indo-Pacific, bleaching began slowly in the Gulf of California in 1987 (Reyes-B. PC) and in Hawaii in 1987 (and in 1986) (Choquette PC), but suddenly in Kenya (McClannhan PC) in 1987.

Only in areas where scientists were closely monitoring corals were details of the sequence of events in bleaching relative to depth available. We suspect that bleaching in most areas was noticed only after many preliminary depth developments were obscured. The limited records show oppos-

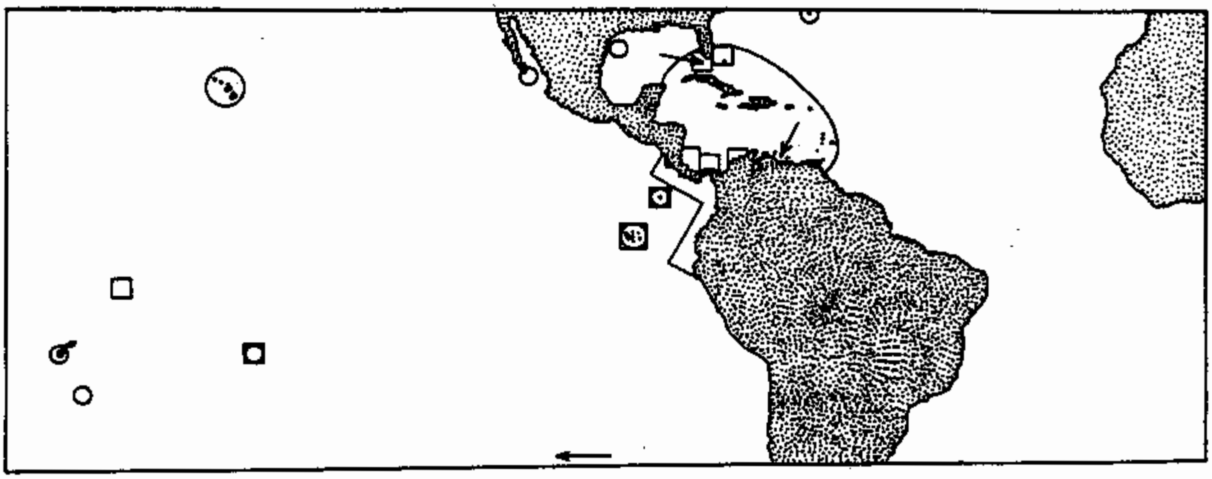


Figure 2: The world from 33°S to 33°N, Part 1: Central Pacific to Atlantic. 1979-80 Coral Reef (Part 1) Bleaching Sites Marked with Arrows, the 1982-83 with Squares and Rectangles, the 1986-88 in Circles and Elipses.

ing trends. In the Florida Keys and Puerto Rico, bleaching started in the shallows and moved deeper; in Jamaica and St. Croix, the opposite was observed (Williams and Bunkley-W., 1989).

Table 1: Photosymbiotic Hosts Which Bleached First.[1]

| SPECIES | LOCATION | DATE | SOURCE |
|---|---|---|---|
| *Acropora cervicornis* | Culebra, Puerto Rico | 1986 | Perkins PC |
| | Looe Key, Florida | 1987 | Causey PC |
| *Acropora palmata* | Looe Key, Florida | 1987 | Causey PC |
| | Puerto Rico | 1989 | Lopez PC |
| *Agaricia agaricites*[2] | Puerto Rico | 1986,<br>1987,<br>1988 | Perez-T. PC |
| *Agaricia lamarcki* | St. Croix, USVI | 1987 | Gladfelter PC |
| *Eunicia* sp. | Turks and Caicos | 1987 | Lott PC |
| *Millepora alcicornis* | Puerto Rico | 1987 | Present paper |
| | Turks and Caicos | 1987 | Lott PC |
| *Millepora complanata* | Puerto Rico | 1987 | Present paper |
| | Turks and Caicos | 1987 | Lott PC |
| *Palythoa caribbea*[3] | Key Largo, Florida | 1987 | Hudson PC |
| | Looe Key, Florida | 1988 | Causey PC |
| *Palythoa mammilosa* | Bermuda | 1988 | Cook PC |
| Gorgonians | Teague Bay, St. Croix, USVI | 1987 | Gladfelter PC |

[1] Williams and Bunkley W. (1989) listed 5 hosts that were first to bleach at 3 Caribbean locations.
[2] Especially sensitive to bleaching in the mangrove habitat.
[3] Gladfelter (PC) noted this host to frequently bleach. Causey (PC) considers it a bleaching "indicator organism". We have frequently noted it to bleach before and after the 1987 event.

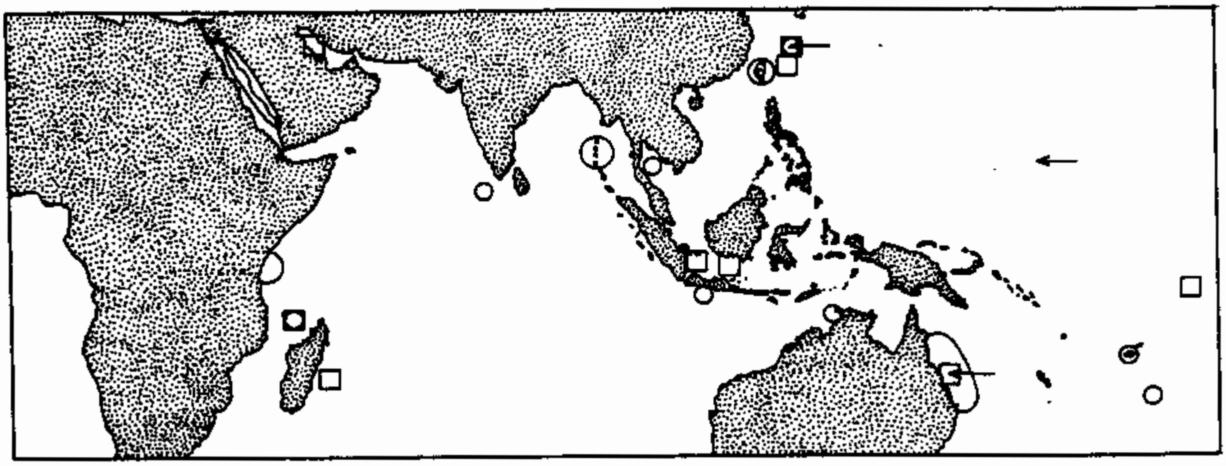
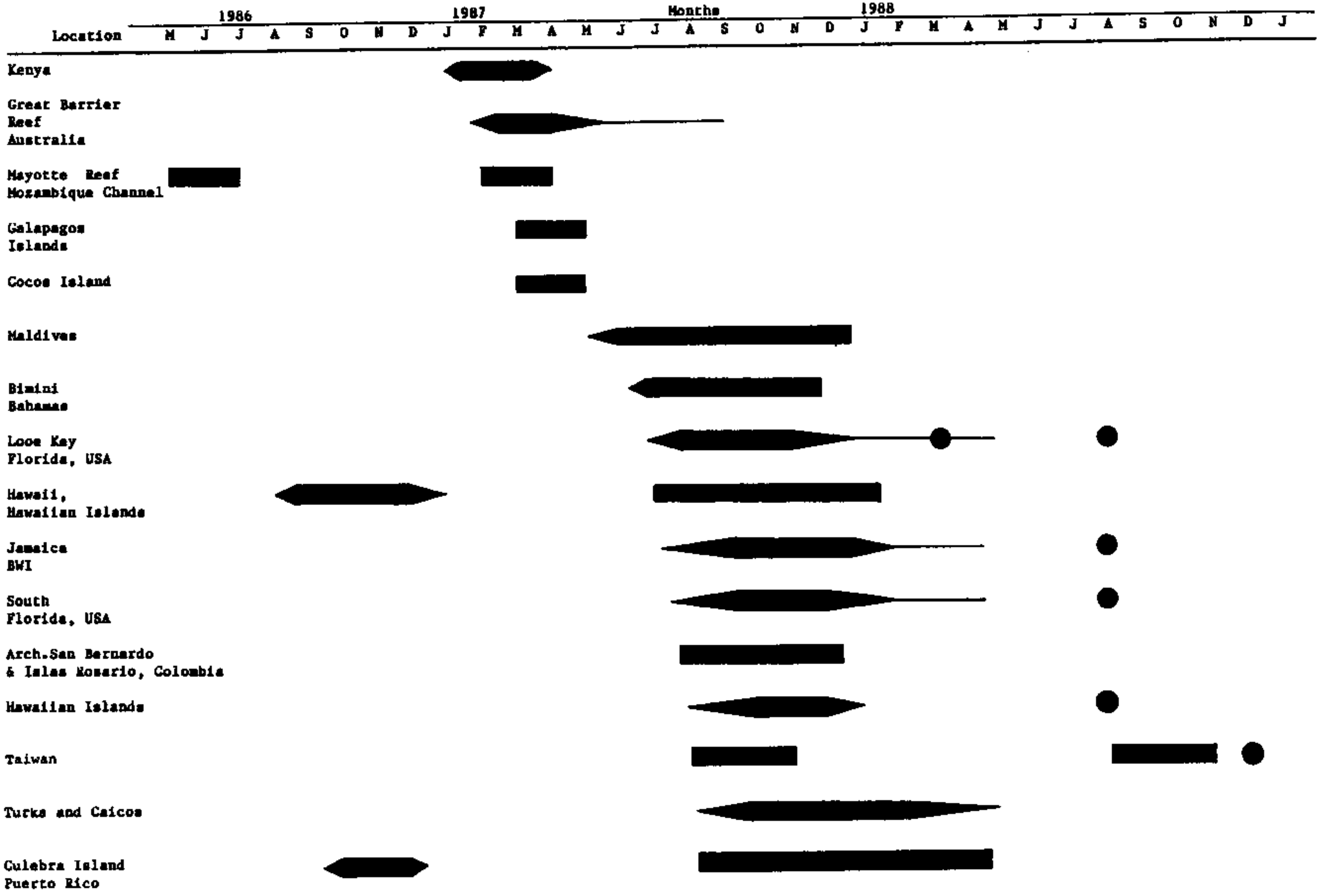
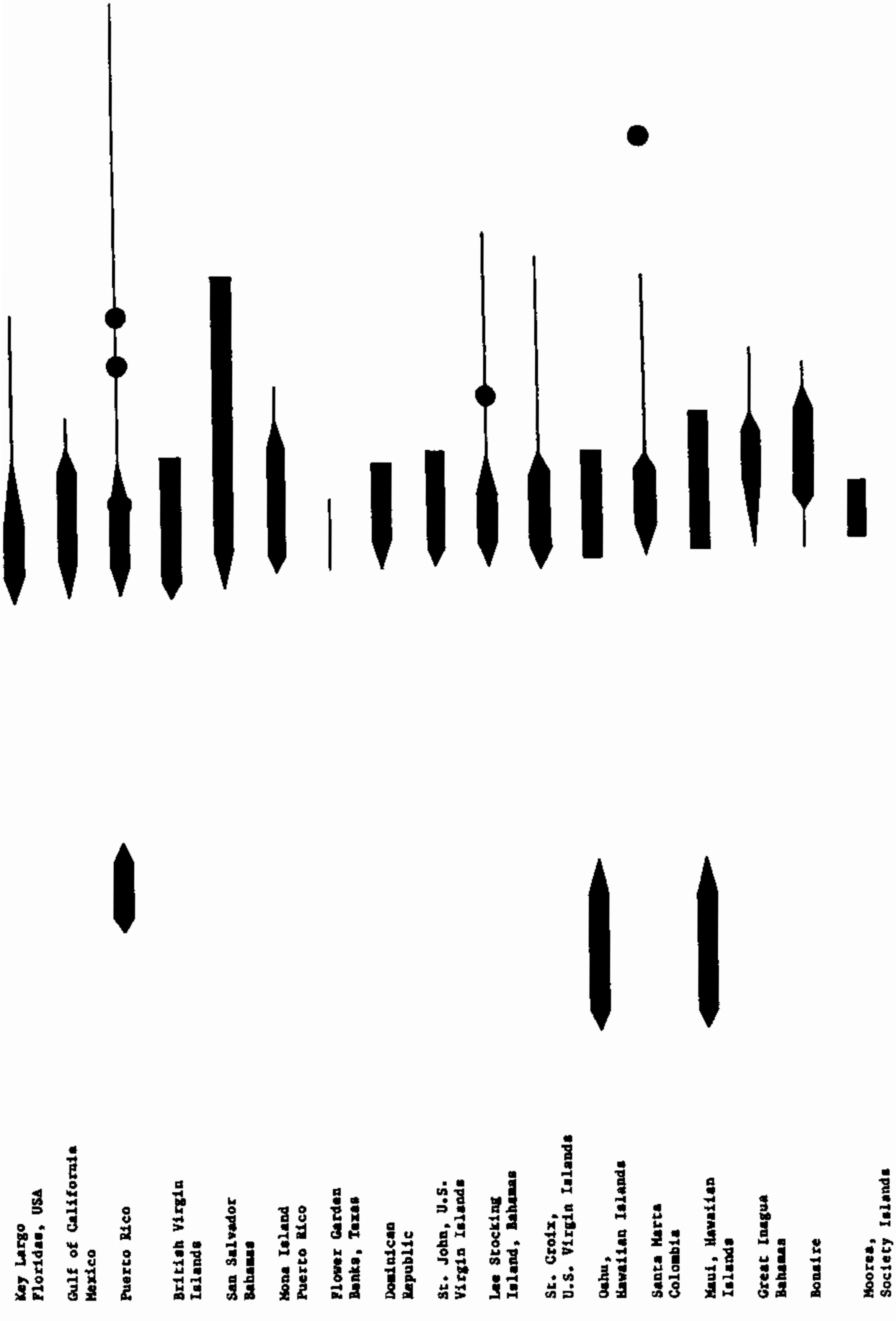
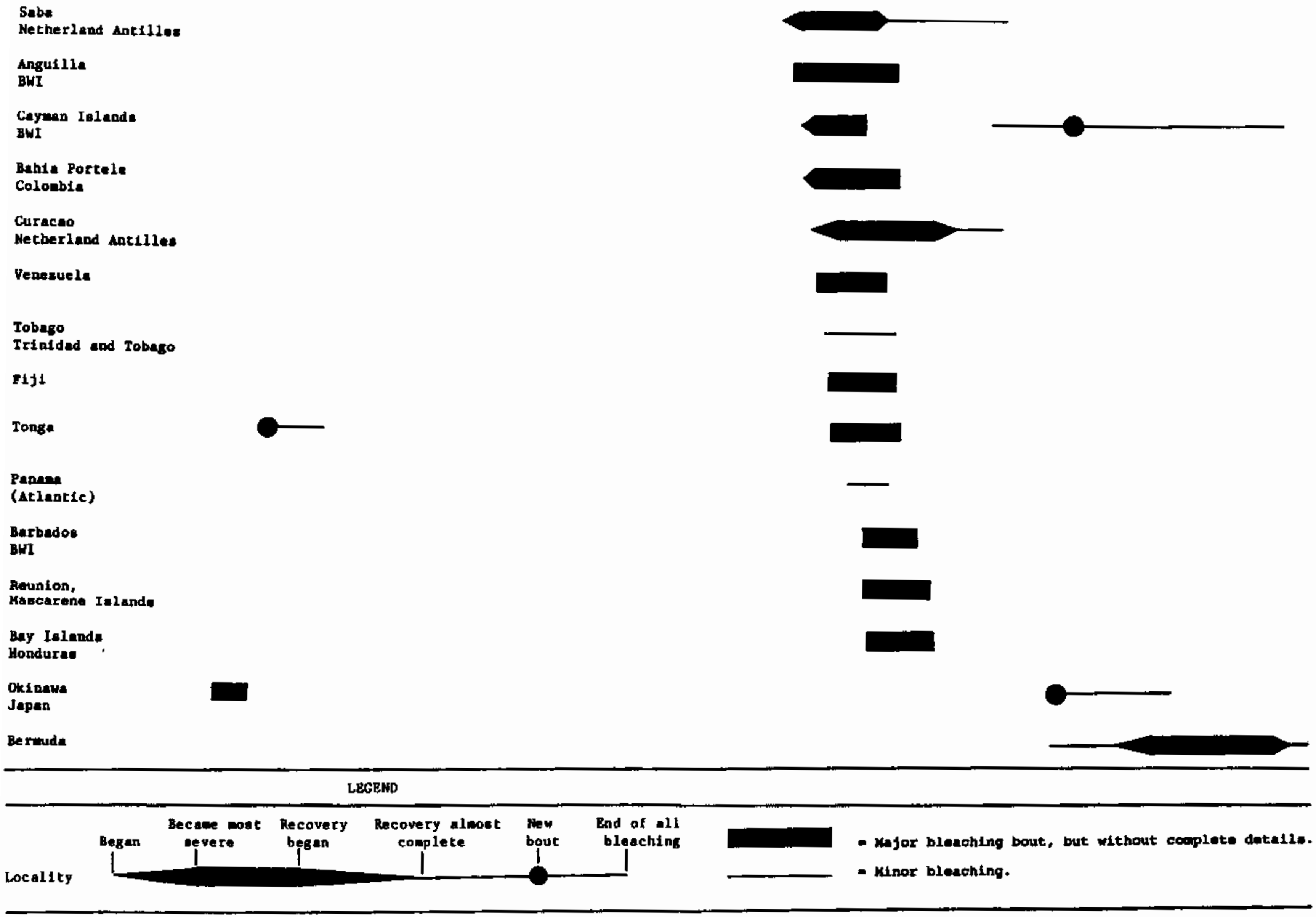


Figure 2: The world from 33°S to 33°N, Part 2: Eastern Atlantic to Western Pacific. 1979-80 Coral (Part 2) Reef Bleaching Sites Marked with Arrows, the 1982-83 with Squares and Rectangles, the 1986-88 in Circles and Elipses.

Figure 3. Progress of the 1986-1988 World-wide Bleaching Events.




Key Largo
Florida, USA
Gulf of California
Mexico
Puerto Rico
British Virgin
Islands
San Salvador
Bahamas
Mona Island
Puerto Rico
Flower Garden
Banks, Texas
Dominican
Republic
St. John, U.S.
Virgin Islands
Lee Stocking
Island, Bahamas
St. Croix,
U.S. Virgin Islands
Oahu,
Hawaiian Islands
Santa Marta
Colombia
Maui, Hawaiian
Islands
Great Inagua
Bahamas
Bonaire
Moorea,
Society Islands


Saba
Netherland Antilles
Anguilla
BWI
Cayman Islands
BWI
Bahia Portele
Colombia
Curacao
Netherland Antilles
Venezuela
Tobago
Trinidad and Tobago
Fiji
Tonga
Panama
(Atlantic)
Barbados
BWI
Reunion,
Mascarene Islands
Bay Islands
Honduras
Okinawa
Japan
Bermuda
LEGEND
Locality
Began
Became most severe
Recovery began
Recovery almost complete
New bout
End of all bleaching
= Major bleaching bout, but without complete details.
= Minor bleaching.

**FOOTNOTE FIGURE 3:** Locations with adequate data to indicate progress of bleaching are arranged in chronological order by the time bleaching began in 1987-1988 (major bout). Last name(s) without dates refer to the Personal Communications List. Those followed by "(date)" refer to References: KENYA=McClanahan; AUSTRALIA=Zann, Oliver; MAYOTTE 1986=Thomassin, 1987=Faure; GALÁPAGOS & COCOS ISLANDS=Glynn (1988b); MALDIVES=Wood (1988); BIMINI=Bland; LOOE KEY=Causey; HAWAII 1986=Choquette, 1987=Brock; JAMAICA 1987=Woodley, Goreau, Sandeman, 1988=Gates; FLORIDA 1987=Szmant, Jaap, 1988=Szmant, Vose; ARCH. SAN BERNARDO & ISLAS ROSARIO=Lang, Bohorquez; HAWAIIAN ISLANDS=Choquette; TAIWAN=Dai; TURKS & CAICOS=Lott,Lang, Manstan; CULEBRA 1986=Perkins, Mignucci-G., 1987=Perkins, Tucker; KEY LARGO=Jaap; GULF OF CALIFORNIA=Reyes-B.; PUERTO RICO 1986 & 1988=Perez-T., 1987=Williams, Bunkley-W.; BRITISH VIRGIN ISLANDS=Keil; Underwater Safaris; SAN SALVADOR 1987=Crawford, Tozer, 1988=Gerace, Hardy; MONA ISLAND 1987=Kontos, Nieves, 1989=Williams, Bunkley-W.; TEXAS=Lang; DOMINICAN REPUBLIC=Geraldes; ST. JOHN=Szmant, Boulon; LEE STOCKING ISLAND 1987=Lang, Wicklund, 1988=Muscato; ST. CROIX=Gladfelter, Hillis; OAHU 1986=Choquette, 1987=Brock; SANTA MARTA=Duque, Zea; MAUI 1986=Choquette, 1987=Brock; GREAT INAGNA=Hardy; BONAIRE=Newton; MOOREA=Richmond; SABA=Hof; ANGUILLA=Lang; CAYMAN ISLANDS 1987=Smith, Sefton; 1988=Hayes & Bush (1989); BAHIA PORTELE=Solano; CURAÇAO=-Sybesma; VENEZUELA=Losada (1988); FIJI=Beckman; TOBAGO 1987=Laydoo, 1988=Boyle; TONGA=Bondurant; PANAMA=Knowlton; BARBADOS 1986=Tomascik, 1987=Hor-rocks; REUNION ISLAND=Naim; HONDURAS=Cruz; OKINAWA 1986=Tsuchiya et al.(1987), 1988=Walker, Muzik, Sakai; BERMUDA=Cook, Hagan & Katz (1988), Katz & Hagan (1989)

## HOSTS AND NON-PHOTOSYMBIOTIC ANIMALS THAT BLEACHED

Williams and Bunkley-W. (1989) noted approximately 84 species of hosts in 3 phyla and 4 orders from 34 countries and/or islands in the Western North Atlantic. The following additional records (Table 2) add 5 species, 2 orders, and 1 country to their (loc. cit.) list.

Table 2: Photosymbiotic Hosts Bleached in the Western North Atlantic.

| SPECIES | LOCATION | DATE | SOURCE |
|---|---|---|---|
| *Agaricia* sp. | Puerto Rico | 1987 | Acevedo PC |
| *Agelas conifera*[1] | Mona Island, PR | 1987 | Kontos PC; Ruetzler PC |
| *Colpophyllia* sp. | Puerto Rico | 1987 | Acevedo PC |
| *Diploria* sp. | Puerto Rico | 1987 | Acevedo PC |
| *Eusmilia fastigiata* | Tobago | 1987 | Risk PC |
| *Hymeniacidon*(?) sp.[2] | Mona Island, PR | 1987 | Kontos PC; Ruetzler PC |
| *Iciligorgia schrammi* | Mona Island, PR | 1987 | Kontos PC; Ruetzler PC |
| *Meandrina meandrites* | Tobago | 1987 | Risk PC |
| *Millepora complanata* | south Florida | 1987 | Ferrer PC |
| | Cuba | 1988 | Ibarra-M. PC |
| *Montastrea annularis* | St. Lucia | 1987 | Lang PC |
| | Grand Bahama Island[3] | 1987 | Waldner PC |
| *Mycetophyllia lamarckiana* | Puerto Rico | 1987 | Goenaga et al., 1989 |
| *Oculina varicosa* | south Florida | 1988 | Vose PC |
| *Plakortis* sp.[4] | Mona Island, PR | 1987 | Kontos PC; Ruetzler PC |
| *Porites astreoides* | St. Lucia | 1987 | Lang PC |
| | Bermuda[5] | 1988 | Hagan and Katz, 1988 |
| *Siderastrea radians* | south Florida | 1988 | Vose PC |
| Unidentified sponges | Puerto Rico | 1987 | Acevedo PC |
| *Xestospongia muta*[6] | Mona Island, PR | 1987 | Kontos PC; Ruetzler PC |

[1] USNM#41423. [2] USNM#41425. [3] Noted by us in a video by Waldner. [4] USNM#41421-41422. [5] Published photograph. [6] USNM#41424.

Table 3: Photosymbiotic Hosts Bleached in the Indo-Pacific.

| SPECIES | LOCATION | DATE | SOURCE |
|---|---|---|---|
| *Acropora* sp. | Maldives | 1987 | Wood 1988 |
| *Acropora* spp.[1] | Andaman Islands | 1989[2] | Wood PC |
| | Okinawa | 1988 | Muzik PC |
| | Fiji | 1988 | Beckman PC |
| Anemones | Maldives | 1987 | Wood 1988 |
| Alcyonarians[3] | Reunion Island | 1988 | Naim PC |
| *Cladiella* sp. | Okinawa | 1988 | Muzik PC |
| Cnidarians[4] | Great Barrier Reef, Australia | 1987 | Oliver PC |
| *Diploastrea heliopora* | Taiwan | 1988[5] | Dai PC |
| *Diploastrea* sp. | Maldives | 1987 | Wood 1988 |
| *Favia* sp. | Maldives | 1987 | Wood 1988 |
| *Favia* spp. | Taiwan | 1988[5] | Dai PC |
| *Favites* spp. | Taiwan | 1988[5] | Dai PC |
| *Favites* sp. | Okinawa | 1988 | Muzik PC |
| Fire corals[6] | Reunion Island | 1988 | Naim PC |
| *Fungia* sp. | Maldives | 1987 | Wood 1988 |
| *Goniastrea* sp. | Maldives | 1987 | Wood 1988 |
| *Leptoseris* sp. | Maldives | 1987 | Wood 1988 |
| *Lobophytum* sp. | Kenya | 1987 | McClanahan PC |
| *Millepora platyphylla* | Taiwan | 1987,1988[7] | Dai PC |
| *Millepora* sp. | Maldives | 1987 | Wood 1988 |
| *Palythoa tuberculosa* | Okinawa | 1988 | Muzik PC |
| *Pavona* sp. | Maldives | 1987 | Wood 1988 |
| | Cocos Island and Galápagos Islands | 1987 | Glynn 1989b |
| *Platygyra* sp. | Maldives | 1987 | Wood 1988 |
| | Okinawa | 1988 | Muzik PC |
| *Platygyra* spp. | Taiwan | 1988[5] | Dai PC |
| *Pocillopora elegans* | Gulf of California | 1987 | Reyes-B. 1988 |
| *Pocillopora meandrina* | Hawaiian Islands | 1987 | Brock PC, Hau PC |
| *Pocillopora* sp. | Maldives | 1987 | Wood 1988 |
| *Pocillopora* spp.[8] | Gulf of California | 1987 | Baynes PC |
| | Hawaiian Islands | 1987 | Choquette PC |
| *Porites* sp. | Maldives | 1987 | Wood 1988 |
| | Cocos Island and Galápagos Islands | 1987 | Glynn 1989b |
| *Seriatopora hystrix* | Taiwan | 1987,1988[7] | Dai PC |
| Soft corals | Maldives | 1987 | Wood 1988 |
| | Kenya | 1987 | McClanahan PC |
| Sponge | Gulf of California | 1987 | Reyes-B. 1988 |
| Stony corals | Kenya | 1987 | McClanahan PC |
| | Reunion Island[9] | 1988 | Naim PC |
| *Stylophora pistillata* | Taiwan | 1987,1988[7] | Dai PC |
| *Stylophora* sp. | Maldives | 1987 | Wood 1988 |
| *Symphyllia* sp. | Maldives | 1987 | Wood 1988 |
| *Tridacna gigas* | Great Barrier reef, Australia | 1987 | Goggin PC |
| *Tridacna* spp. | Great Barrier reef, Australia | 1987 | Lucas PC |

[1] and other damage caused by bleaching. [2] February. [3] a few.
[4] 30 species almost the same as in Oliver (1985). [5] November. [6] Some. [7] July to September.
[8] All species in this genus bleached. 80% of the coral cover was affected. [9] 20%.

Gladfelter (PC) felt that not all of the species of reef corals in St. Croix bleached. We could find bleached examples of every reef coral species we could identify during the most intense period of bleaching in Puerto Rico. The bleaching may have been more extensive in Puerto Rico than St. Croix. Most reports that we received concentrated on either the most abundant or most bleached local hosts and made no attempt to determine all species bleaching.

A non-photosymbiotic coral, *Stylaster roseus* and the non-zooxanthellate pigments (orange) in a sponge, *Mycale laevis*, bleached (Williams, L. and Williams, 1988; and Williams and Bunkley-W., 1989). The photosymbiotic microorganisms of *Xestospongia muta* and possibly other sponges which bleached are cyanobacteria, not zooxanthellae (Vicente PC). The pigments in 1 monitored *M. laevis*, which bleached before September 1987 off La Parguera, Puerto Rico, returned to the sponge between March 1988 and March 1989. The comments of unknown reviewers (Proc. 6th Intern. Coral Reef Sympos.) that *S. roseus* could not bleach were considered, but a description of many live colonies gradually turning to white along closely monitored transects (Kontos PC) was difficult to dispute. Subsequent observations by the authors at Mona Island suggest that populations of *S. roseus* have drastically reduced, substantiating Kontos' suggestion that these hydrozoans were severely affected by the bleaching event.

Forty-two species were reported not bleached at various western Atlantic locations (Williams and Bunkley-W., 1989). Most of these were reported bleached at other locations or even at the same general location by other observers. Most species were noted unbleached only in single reports.

Table 4: Hosts Not Bleached in 1987 (Only Atlantic Species with Multiple Reports).

| SPECIES | LOCATION | SOURCE |
|---|---|---|
| *Acropora palmata* | Bahamas[1], Colombia[1], Florida<br>Florida Keys,[1] Jamaica,[1] Venezuela | Williams & Bunkley-W. 1989 |
| | Mona Island[2] | Nieves PC |
| *Dendrogyra cylindrus* | Jamaica, British Virgin Islands | Williams & Bunkley-W. 1989 |
| | Mona Island | Nieves PC |
| *Pavona clivosa*[3] | Gulf of California | Reyes-B. PC |
| *Pavona gigantea*[3] | Gulf of California | Reyes-B. PC |
| *Pavona* spp.[3] | Kenya[4] | McClanahan PC |
| *Porites californica*[3] | Gulf of California | Reyes-B. PC |
| *Porites* spp.[3] | Kenya[4] | McClanahan PC |
| *Psammocora stellata*[3] | Gulf of California | Reyes-B. PC |
| Sea anemones | Great Barrier Reef, Australia | Oliver PC, Zann PC |
| | Gulf of California | Reyes-B. PC |
| Soft corals | Gulf of California | Reyes-B. PC |
| Sponges | Great Barrier Reef, Australia | Oliver PC, Zann PC |

[1] Reported bleached by others at these locations. [2] *A. palmata* also partially bleached at Mona Island and Puerto Rico during the 1989 bout. [3] Most common stony corals in area.
[4] Although 20% of the total stony coral cover was bleached.

*Acropora palmata* was reported bleached in 40% of the locations in the Atlantic and was the 6th most reported among 84 species noted by Williams and Bunkley-W. (1989). Jaap (in Hollings 1988) suggested *A. palmata* did not bleach during the 1983 event and was little bleached in 1987. At Grecian Rocks in the Florida Keys, no *A. palmata* bleached (Jaap, 1988). Hudson (1988) found only moderate bleaching in *A. palmata* (uniformly reduced intensity of color) in the Florida Keys in 1987. Jaap (in Hollings, 1988) and Nieves (PC) suggested that *A. palmata* was one of the least affected or most resistant species. Our observations in Puerto Rico would agree. It was often found unaffected and the colonies affected were in what might be considered an interrupted bleaching state with large, white, irregular blotches (Williams, L. and Williams, 1988) on a normal or slightly lighter than normal background. Rarely, these blotches would cover 60-80% of a colony, but usually much less. Some possessed totally white terminal branches of 10-20% of a colony, but no totally bleached colonies were noted. Lang (PC) also found *A. palmata* much less affected in the Bahamas than the similar *A. cervicornis*. Sandeman (1988b) demonstrated in experiments that *A. palmata* is able to regulate its zooxanthellae more effectively than other corals and can withstand higher levels of light and temperature without bleaching. Despite *A. palmata* being frequently noted not to bleach or to bleach only slightly and *A. cervicornis* noted not bleached only once (Hudson, 1988), bleaching of these 2 species is closely coupled in our reports. They occur bleached together in 13 locations, with each occurring alone only once. Their bleaching seems at least circumstantially related.

*Dendrogyra cylindrus* was noted bleached only in 3 (Puerto Rico, Culebra Island, and St. Thomas) of 35 Atlantic locations (Williams and Bunkley-W., 1989). Nieves (PC) considered this species resistant to bleaching on Mona Island. In Puerto Rico, we rarely found it bleached, and bleaching was in small discolored to white patches on the sides of colonies. We suspect that the prominent and easily recognizable colonies of this coral would not have been overlooked in so many areas, if it had been bleached.

## SMALL SCALE FEATURES

Some western Atlantic corals began bleaching on their edges or top and progressed inward or downward, others began at their bases and moved upwards (Williams and Bunkley-W., 1989). A colony of *Acropora cervicornis* in a public aquarium in St. Thomas bleached from the bottom up to the top overnight (3 May 1988) (Nunn PC). In the Indian Ocean, *Acropora* spp. of the Andaman Islands bleached from their bases toward the tips (Wood PC). This is similar to the action seen in white band disease, but the progress of this disease is usually slower than that seen in bleaching. In the Pacific, *Pocillopora* spp. in Hawaii 1987 (and 1986) (Choquette PC) and *P. elegans* in the Gulf of California in 1987 (Reyes-B. PC) began bleaching at the tips and progressed inward and down to the base. *Tridacna gigas* specimens on the Great Barrier Reef bleached in the central portion of the mantle, but retained color on the extreme outer margin (Goggin PC). Other Caribbean hosts became blotched or striped tan and brown or white and tan, before bleaching white; or gradually became uniformly lighter in color (Hudson, 1988; Williams and Bunkley-W., 1989). Some colonies never progressed beyond the patterns described above, possibly because the bleaching process was arrested. These forms were probably less damaged than their "totally" bleached neighbors. Another possible explanation for the various patterns is that different hosts presumably have different strains of zooxanthellae with different physiological tolerances (Gladfelter, 1988). Also, different strains of zooxanthellae may even occur in different parts of the same colony (Sandeman, 1988b).

Table 5: Bleaching of Some Corals Revealed Delicate Colors Normally Concealed by the Color of the Zooxanthellae.

| SPECIES | LOCATION | DATE | COLOR | SOURCE |
|---|---|---|---|---|
| *Acropora* spp. | Fiji | 1988 | Glowing-blue | Beckman PC |
| *Montastrea annularis* | Dominican Republic | 1987 | Lavender-blue | Geraldes PC |
| *Porites astreoides* | Colombia | 1987 | Yellow | Lang PC |
| | Mona Island, PR | 1988 | Yellow | This Paper |
| | St. Thomas, USVI | 1989 | Bright Blue | This Paper |
| *Porites porites* | Colombia | 1987 | Yellow | Lang PC |
| *Siderastrea radians* | Caribbean | 1987 | Lavender-blue | Williams & Bunkley-W. 1989 |
| *Siderastrea siderea*[1] | Caribbean | 1987 | Lavender-blue[2] | Williams & Bunkley-W. 1989 |
| *Solenastrea bournoni* | Colombia | 1987 | Lavender-blue | Williams & Bunkley-W. 1989 |

[1] Williams, L. and Williams (1988, p. 85) illustrated a lavender specimen from Puerto Rico.

[2] Acevedo and Goenaga (1986) did not note this color in Puerto Rican bleached specimens in 1985.

The number of individuals bleached within a species, and the amount of surface area bleached from the reports received were used by Williams and Bunkley-W. (1989) to determine that the most intensely bleached areas in the Atlantic were the northern Caribbean, Bahamas and south Florida. Subsequent reports we received agreed with the original analysis. No obvious large-scale patterns were evident in the Indo-Pacific records noted below (Table 6).

Table 6: Proportion of Colonies Bleached of Indo-Pacific Host Species and Areas Affected.

| COLONIES BLEACHED IN A SPECIES | SURFACE AREA BLEACHED | LOCATION | DATE | SOURCE |
|---|---|---|---|---|
| 20-100% (50% of many, 80-100% of some)[1] | 20-100% (most 100%) | Australia | 1987 | Oliver PC |
| From virtually all to only isolated[1] | 20-100% (most 100%) | Australia | 1987 | Zann PC |
| 80% (soft corals) | 100% | Kenya | 1987 | McClanahan PC |
| 20% (stony corals) | 20-100% | Kenya | 1987 | McClanahan PC |
| Large-scale bleaching | | Moorea | 1987 | Richardson PC |
| 15% of *Pocillopora elegans* | 100% | Gulf of California | 1987 | Reyes-B. PC |
| Unidentified sponges | 9% | Gulf of California | 1987 | Reyes-B. PC |
| 80% of *Pocillopora* spp. | | Gulf of California | 1989 | Baynes PC |
| 5-10% of *P. meandrina* | 100% | Hawaiian Islands | 1987 | Brock PC |
| 10% of *P. meandrina* | | Hawaiian Islands | 1987 | Hau PC |
| 80% of *Pocillopora* spp. in some areas | | Hawaiian Islands | 1987 | Choquette PC |

[1]Highly variable between sites.

In a world-wide bleaching event in summer-fall 1988, which was much less severe and intense than the earlier 1987 bouts, fewer hosts and less surface areas were affected. Williams and Bunkley-W. (1989) found that the geographic areas in the greater Caribbean with the highest percentage of colony surfaces bleached were also the areas in which bleaching occurred first.

Table 7: Percentage of Total Coral Cover Bleached.

| % TOTAL COVER | LOCATION | DATE(S) | SOURCE |
|---|---|---|---|
| 80-100 | Mangroves of S.W. Puerto Rico | 1986, 1988 | Perez-T. PC |
| 10-15 | Gulf of California | 1987 | Reyes-B. PC |
| 75-100 | Okinawa | 1987 | Muzik PC |
| 20-100 | Kenya | 1987 | McClanahan PC |
| 5-60[1] | Australia | 1987 | Zann PC |
| 20-50[1] | Australia | 1987 | Oliver PC |

[1]Highly variable between sites.

Some interesting differences occurred between the supposedly very similar *Millepora alcicornis* and *M. complanata* in the southern Caribbean. In Venezuela, similar numbers of each species bleached (50 and 60% out of 200 and 100 colonies respectively) but most *M. alcicornis* totally bleached, while most *M. complanata* only partially bleached (Losada, 1988). High percentages of *M. alcicornis*, but not *M. complanata* also died in some areas of Colombia (Solano-P. PC).

Table 8: Species Most Often or Severely Bleached or Most "Susceptable" to Bleaching.

| SPECIES | LOCATION | DATE | SOURCE |
|---|---|---|---|
| *Acropora cervicornis*[1] | Bahamas | 1987 | Lang 1988a,c |
| *Acropora palmata*[1] | Florida Keys | 1987 | Jaap 1988 |
| *Agaricia* spp.[2] | Caribbean | 1987 | Williams & Bunkley-W. 1989 |
| *Diploria labyrinthiformes*[3] | Jamaica | 1987 | Woodley 1988 |
| *Diploria* sp.[3] | Mona Island, Puerto Rico | 1987 | Nieves PC |
| Faviids[4] | Taiwan | 1987 | Dai PC |
| *Millepora alcicornis* | Bermuda | 1988 | Cook PC |
| *Millepora platyphylla*[5] | Taiwan | 1987 | Dai PC |
| *Millepora* spp.[2,6] | Caribbean | 1987 | Williams & Bunkley-W. 1989 |
| *Montastrea annularis*[2] | Caribbean | 1987 | Williams & Bunkley-W. 1989 |
| *Montastrea cavernosa*[3,7] | Jamaica | 1987 | Sandeman 1988b |
| *Palythoa caribbea*[2] | Caribbean | 1987 | Williams & Bunkley-W. 1989 |
| *Porites astreoides*[3] | Mona Island, Puerto Rico | 1987 | Nieves PC |
|  | Bonaire | 1979 | Hof PC |
| *Porites porites*[3] | Mona Island, Puerto Rico | 1987 | Nieves PC |
| *Seriatopora hystrix*[5] | Taiwan | 1987 | Dai PC |
| *Siderastrea siderea*[3,7] | Jamaica | 1987 | Sandeman 1988b |
| Soft corals | Kenya | 1987 | McClanahan PC |
| *Stylophora pistillata*[5] | Taiwan | 1987 | Dai PC |

[1] Possibly complicated by White Band Disease. [2] These species, representing 3 cnidarian orders, were also similarly listed in most reports received after the Williams and Bunkley-W. (1989) paper. [3] Among others we also listed above (footnote #2). [4] Low temperatures. [5] High temperatures. [6] Although Sandeman (1988) and Woodley (1988) found few *Millipora* spp. bleached in Jamaica. [7] Not listed by Woodley (1988) as most bleached in Jamaica.

## LARGE SCALE FEATURES

Williams and Bunkley-W. (1989) simply summarized the maximum depths where bleaching was found in the greater Caribbean as the approximate limits of zooxanthellae. Most of the maximum depth estimates available were subjective observations by SCUBA divers from shallow depths. Later submersible and remote operated vehicle (ROV) observations corroborate deeper records (Table 9). These exact observations cannot rule out bleaching at even greater depths as the most severe bleaching had ended before the submersible and ROV observations were made. The small number of observations below 60 m in Puerto Rico may have missed the fewer colonies bleached at these depths. Smith (PC) found few below 60 m and Lang (PC) found approximately 3% of the colonies bleached at 91.4 m. Indo-Pacific reports did not relate depths of bleaching to the total depth range of hosts present; therefore, it is not clear if bleaching was depth related (Table 9).

Most of our reports and Bohorquez (1988), Jaap (1988) Jaap in Hollings (1988), Knowlton (1988) Lang (1988a,c) and Lang in Hollings (1988) indicate either uniform bleaching in shallow to moderate depths or more intense bleaching in the shallows. Other reports indicate a great variation in local bleaching patterns (Table 10).

Some of the patterns of bleaching around islands (Table 11) may be due to distribution of corals rather than bleaching. Most coral reefs and most SCUBA diving in Barbados occurs along the west coast; therefore, most reports would be expected to originate from this area. However, Vicente (PC) was able to confirm bleaching along the north coast of Puerto Rico, where few corals exist, by the presence of intensely bleached, white *Xestospongia muta*. Muzik (PC) noted that many

Table 9: Depths of Bleaching in 1987.

| DEPTH (METERS) | LOCATION | SOURCE |
|---|---|---|
| CARIBBEAN | | |
| 1-40 | Caribbean | Williams et al. 1987 |
| 1-60 | Caribbean | Williams & Williams 1987 |
| 60.0 | Southwestern Puerto Rico[1] | Bunkley-W. unpub. data |
| 73.2[2] | Lee Stocking Island, Bahamas | Wicklund in Hollings 1988 |
| 85.3 | Cayman Islands | Smith PC |
| 91.4 | Lee Stocking Island, Bahamas[3] | Lang PC |
| INDO-PACIFIC | | |
| to 2 | Kenya | McClanahan PC |
| 0-6 | Great Barrier Reef, Australia | Oliver PC |
| to 13 | Mayotte Islands | Thomassin PC |
| 3-15 | Gulf of California | Reyes-B. 1988 |
| to 20 | Hawaii | Brock PC |
| 1-21 | Hawaii | Hau PC |
| Shallow to 30 | Maldives | Wood 1988 |
| 1-40 | Great Barrier Reef, Australia | Zann PC |
| Down to 45 | Hawaii | Choquette PC |

[1] Remote operated vehicle operations. [2] Based at least partially on bleached sponges and there is some question whether sponges which are normally photo-symbiotic in the shallows possess these photosymbionts below 37m (Vicente PC). [3] Submersible operations.

Table 10: Most Intensely Bleached Habitats or Depth Ranges.

| SITUATION | LOCATION | DATE | SOURCE |
|---|---|---|---|
| Intertidal areas | Moorea | 1987 | Richmond PC |
| Intertidal areas | Okinawa | 1987 | Sakai PC |
| Lagoonal areas | Kenya | 1987 | McClanahan PC |
| Lagoon and shallows | Fiji | 1988 | Beckman PC |
| Lee sides of reefs | Culebra Island, PR | 1987 | Perkins PC |
| Intermediate depths | St. Croix, USVI | 1987 | Gladfelter PC |
| Intermediate depths[1] | Jamaica | 1987 | Smit.-V. PC |
| Intermediate depths | Grand Turk[2] | 1987 | Harrigan PC |
| Intermediate depths | Cuba | 1988 | Alcolado PC |
| Intermediate depths | Tobago[3] | 1988 | Boyle PC |
| Increasing with depth to 14 m | Culebra Island, PR | 1987 | Tucker PC |
| Increasing with depth to 55 m | Bahamas | 1987 | Lang 1988a,c & Lang in Hollings 1988 |
| Fore-reef slopes | Culebra Island, PR | 1987 | Tucker PC |
| Ocean fore-reef[4] | Jamaica | 1987 | MacFarlane & Goreau 1988 |
| Deeper, drop-off areas[5] | Turks and Caicos | 1987 | Lott PC |
| Uniform at all depths | Maldives | 1987 | Wood 1988 |

[1] At some sites. [2] Turks and Caicos. [3] Trinidad and Tobago.
[4] Twice as intense as on the protected back reef. [5] Less bleaching in shallows.

areas of the coast in Okinawa cannot bleach because no live corals remain. A rumor has also been received about bleaching along 1 side of Malaysia and not the other. Unfortunately, no details are available to substantiate this pattern (Halas PC, Lang PC).

Table 11: Patterns of Bleaching Around Islands or in Island Chains.

| SIDE(S) | LOCATION | DATE | SOURCE |
|---|---|---|---|
| South coasts[1] | Cayman Islands | 1987 | Williams & Bunkley-W. 1989 |
| South coast[1] | Culebra Island, PR | 1987 | Williams & Bunkley-W. 1989 |
| South coast | Maui, Hawaiian Islands | 1987 | Hau PC |
| Southernmost island[1] | Hawaiian Chain | 1987 | Brock PC |
| North coast[1] | San Salvador, Bahamas | 1987 | Gerace PC |
| West coast | Barbados | 1987 | Horrocks PC |
| West coast | Hawaii, Hawaiian Islands | 1987 | Hau PC |
| West coast[1,2] | Maldives | 1987 | Wood PC |
| All but east coast | Bonaire | 1979-80 | Hof PC |
| All but southeast | Mona Island, PR | 1987 | Kontos PC |

[1] More intensely bleached.
[2] Some, but not all reports supported this pattern on western sides of atolls.

The opposing inshore/offshore patterns of bleaching in Venezuela and Panama at the same time are perplexing (Table 12). The coral reefs along the eastern Pacific were so devastated by the 1983 bleaching and other impacts which followed (Glynn, 1984a,b; 1985a,b; 1988b) that few hosts may be available in many areas to indicate bleaching. However, some reports would be expected and we received none along this coast for 1987-88, except in the Gulf of California. Lang in Hollings (1988) suggested that the early bleaching in Florida and western Caribbean coast of Colombia (Table 12) was due to more "artificial stresses" on continental reefs in comparison with insular areas. Additional data (Fig. 4) suggest that the Caribbean coast of Colombia was possibly not one of the earliest areas to bleach, but it remains the only Atlantic area out of south Florida, Bahamas and the northern

Table 12: Inshore vs. Offshore Bleaching Patterns.

| INSHORE | OFFSHORE | LOCATION | DATE | SOURCE |
|---|---|---|---|---|
| +[1] | – | Australia | 1987 | Oliver PC, Zann PC |
| +[2] | –[3] | West Indies | 1987 | Lang in Hollings 1988 |
| –[4] | + | Florida Keys | 1987 | Hunt PC |
| –[2] | +[5] | Central America | 1987 | Glynn 1988b,1989b |
| – | +[6] | Barbados | 1987 | Horrocks PC |
| + | – | Venezuela | Late 1987 | Williams & Bunkley-W. 1989 |
| – | +[7] | Panama (Caribbean) | Late 1987 | Williams & Bunkley-W. 1989 |
| – | +[1] | Bermuda | 1988 | Cook PC |

[1] More bleached. [2] Continental coasts, early bleaching. [3] Insular areas. [4] Less bleached.
[5] Galápagos and Coco Islands. [6] Bank reefs. [7] San Blas Islands.

Caribbean which bleached intensely in the 1987 event. The mix of inshore/offshore data suggests the importance of local conditions or local effects in the 1987-88 portion of the event, and the perplexing variability which characterizes this disturbance.

Geographic spreading in this event must remain unconfirmed. It is a process which was unfortunately beyond the scope of the then existing small-scale experimental work (Table 13). Woodley (1988) noted reports of bleaching at Montego Bay to the west of Discovery Bay on the north coast of Jamaica and at Port Royal on the south coast in December 1987. This might indicate spreading, but Smit-V. (PC) noted bleaching at Montego Bay and other areas on the north coast in mid-September 1987. No reports suggested geographic spreading of this event in the Indo-Pacific. The bleaching in 1987 (and 1986) in the Hawaiian Islands seemed to begin on all the islands at approximately the same time (Choquette PC).

Table 13: Geographic Spreading of Bleaching.

| MOVEMENT | LOCATION | DATE | SOURCE |
|---|---|---|---|
| South to north | Bahamas | 1987 | Williams & Bunkley-W. 1989 |
| South to north | Florida Keys to south Florida | 1987 | Williams & Bunkley-W. 1989 |
| South to north | Looe Key to Dry Tortugas | 1987 | Jaap 1988 |
| North to south | Looe Key to West Palm Beach | 1987 | Jaap 1988 |
| West to east | north coast of St. Croix | 1987 | Williams & Bunkley-W. 1989 |
| West to east | Colombia to Venezuela | 1987/88 | Williams & Bunkley-W. 1989 |
| North coast to off shore | from St. Croix to Buck Island[1] (north of western end) | 1987 | Hillis PC |

[1] Noted more than a month after the north coast of St. Croix.

Our suggestion that the 1987-88 events were, overall, the most extensive and severe ever reported is based on a combination of parts of many reports. In some cases local observers suggested that the event was the largest ever (Table 14). An unconfirmed report of bleaching was received from the north coast of Australia at Darwin (Zann PC). Bleaching was not documented from other areas of the north coast, but few observations were made during the time of this event in those remote areas.

Table 14: Most Severe and Extensive Bleaching Ever Reported.

| LOCATION | DATE | SOURCE |
|---|---|---|
| Atlantic | 1987-1988 | Williams & Bunkley-W. 1989 |
| Great Barrier Reef, Australia | 1987[1] | Zann PC |
| North coast of Australia | 1987 | Zann PC |
| Maldives | 1987 | Wood 1988 |
| Hawaiian Islands | 1986, 1987 | Choquette PC |
| Florida reef track | 1987 | Causey PC, Jaap PC |
| Bahamas | 1987 | Wicklund PC |

[1] May be the most extensive.

The potential extent of bleaching in the eastern Pacific in 1987 and Okinawa in 1988 will never be known because many of the more sensitive hosts were already dead. This may be true of other areas of the Indo-Pacific, or possibly, bleaching there was either less severe or less completely reported (Fig. 2). Judging from the reports of bleaching, surface areas of reef affected, number and percentage cover of colonies, and tissue loss and mortalities, the north central Caribbean, Bahamas, and south Florida seemed to be the most intensely bleached Atlantic area in 1987-88. All of the Florida reef tract from West Palm Beach through the Dry Tortugas was affected (Causey, 1988; Jaap, 1988). As early as 10 November 1987, Dill in Hollings (1988) noted bleaching all through the Bahamas. Reports we received later from all of the major Bahamian Islands confirmed his statement. Bleaching occurred all around Puerto Rico, Mona Island, Culebra, and Vieques in 1987-88. Most coral reefs in the British Virgin Islands were bleached. Where observations were made in the Dominican Republic, bleaching was intense and extensive (Geraldes PC). Early in the bleaching event, incomplete reports of intense and extensive bleaching were received from Cuba and Haiti. More information is needed from these areas. Bleaching in the remainder of the greater Caribbean area was less intense and less damaging. Bleaching in these areas (with the exception of the Flower Garden Banks off Texas and the western Colombian Caribbean coast) began in late November 1987 and continued to early January 1988. Despite reports (Palca, 1987; Jaap in Hollings, 1988, Weicker in Hollings, 1988, Wicklund in Hollings, 1988) of bleaching in Bermuda in 1987 (questioned by Lang in Hollings, 1988), no bleaching occurred there. The coral reefs of Bermuda were closely monitored in 1987 and 1988, and no bleaching occurred there until mid-1988 (Cook PC).

The concentration of the first bout in a limited portion of the greater Caribbean region (Table 15) indicates some relationship among these sites or the focusing of some phenomenon which caused the bleaching in this area. After November-December 1987, a less intense, but more widespread effect prevailed. Understanding what these original, diverse areas had in common during this period

Table 15: Bouts of 1987-1988 Events and Additional Bouts in 1989 in Greater Caribbean Area with Some Corresponding Bleaching Noted from the Indo-Pacific.

| LOCATION<br>SOURCE | DATE | |
|---|---|---|
| **BOUT 1 - Most Intense Bleaching - Restricted areas** | | |
| Northern Caribbean<br>Bahamas<br>South Florida<br>Texas[1]<br>Colombia[1] | July to early November 1987 | Williams & Bunkley-W. 1989 |
| **BOUT 2 - Less Intensive - Wider Areas** | | |
| Remainder of the West Indies including original areas | November 1987 to January 1988 | Williams & Bunkley-W. 1989 |
| **BOUT 3 - Much Less Intense Bleaching -Few Areas (or little noted?) - cool water period** | | |
| Puerto Rico[2] | February-April 1988 | Williams & Bunkley-W. 1989 |
| Bahamas (Lee Stocking)[2] | | Lang PC |
| St. Thomas | | Nunn PC |

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**BOUT 4 - Moderate to Less Intense Bleaching - Wide Spread Warm Water Period**

| | | |
|---|---|---|
| Bahamas | Summer-Fall 1988 | Muscato PC |
| Bermuda | | Cook PC |
| Cayman Islands | | Hayes & Bush 1989 |
| Colombia | | Zea PC |
| Cuba | | Alcolodo PC |
| Florida Keys | | Causey PC |
| South Florida | | Szmant PC |
| Jamaica | | Gates PC |
| Panama (inshore) | | Soong PC |
| Peter Island and Virgin Gorda, British Virgin Islands | | Kohler PC |
| St. Croix, USVI | | Gladfelter PC |
| St. John, USVI | | Kohler PC |
| St. Lucia | | Lang PC |
| St. Thomas, USVI | | Nunn PC |
| Tobago, Trinidad and Tobago | | Boyle PC, Risk PC |
| Puerto Rico | | Present paper |

**Corresponding Bleaching in the Indo-Pacific.**

| | | |
|---|---|---|
| Fiji | Summer-Fall 1988 | Beckman PC |
| Hawaii | | Choquette PC |
| Indonesia | | Tomascik PC |
| Ishigaki Island, Japan | | Muzik PC |
| Okinawa | | Muzik PC, Sakai PC, Walker PC |

**MINOR BOUT Very Extensive but Moderate Bleaching**
**(only noted where corals were very closely monitored) - Cool Water Period**

| | | |
|---|---|---|
| St. Thomas | March-April 1989 | McLain PC |
| Mona Island, Puerto Rico | | This paper |
| Southwestern Puerto Rico | | This paper |

**Corresponding Bleaching in the Pacific**

| | | |
|---|---|---|
| Gulf of California[3] | March 1989 | Baynes PC |

[1] Less intense bleaching at same time. [2] Areas intensely monitored at this time.
[3] Very intense and extensive bleaching.

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of intense bleaching might help explain this bleaching event. This pattern might indicate a physical effect centered first on the northern Caribbean, Bahamas and south Florida, but later expanding to include all of the greater Caribbean and eastern Pacific. But a simple stimulus would not explain why the secondary bout also occurred in some of the previously unbleached hosts in the most severely affected areas, unless the focused and the more diffuse effects were the same phenomenon and the combined long-term exposure finally overcame more resistant hosts. What this focused portion of the event does show is a regional intensification by some as yet undefined effect. Although the most intense bleaching occurred during the normal, warmestwater period of the year and some inshore temperatures were unusually high, sea surface temperatures of the greater Caribbean region showed nothing unusual (Atwood et al., 1988). The summer-fall 1988 bleachings may be a separate event, even though bleaching continued at reduced levels throughout 1987-88 at many locations. Whether bleaching continued from the original bout or continued from the intermediate bouts was not clear from our reports. Transect studies coordinated by Lang (PC) may be of more use in answering this question.

A minor amount of natural or "background" bleaching occurs on coral reefs (Table 16).

Table 16: Natural or Background Bleaching Occurring at Low Levels.

| LOCATION | TIME PERIOD | LEVELS | SOURCE |
|---|---|---|---|
| **CARIBBEAN** | | | |
| Jamaica (2 sites) | Prior to 1987 | very low | Williams & Bunkley-W. 1989 |
| Colombia | Prior to 1987 | very low | Williams & Bunkley-W. 1989 |
| Puerto Rico | Prior to 1987 | anemones[1] | Ballantine PC |
| St. Croix | Last 10 years | *Palythoa caribbea* frequently | Gladfelter PC |
| **INDO-PACIFIC** | | | |
| Great Barrier Reef, Australia | Common | corals[1] | Fisk & Done 1985 |
| Iriomoto Island, Japan | 1987 | anemones[1] | Yokochi PC |
| Maldives | Last 15 years | very low | Wood 1988 |
| Fiji | Long-term | very low | Beckman PC |

[1] Isolated bleached.

We believe the bleaching (Bouts #2-4, Table 15), after recovery began in many areas, was in excess of "background" bleaching and represented new bouts (or events) of the 1987-88 complex. Recent minor bleaching, usually on a seasonal basis, may have significance in the current events and will be considered later.

Knowing when and where bleaching was absent (Table 17) is almost as important in understanding the patterns and causes of the 1987-88 events as knowing when and where it happened. Unfortunately, few observers were willing to send negative reports. The interpretation of this information is also more difficult. Due to the high variability of the event among localities and even habitats, bleaching may have been missed in limited or casual observations. Hosts can sometimes bleach and recover in 4 weeks (Glynn, 1988b; Tomascik PC); therefore, even a thorough photo-transect at monthly intervals could, theoretically, miss a minor bout. For example, bleaching seems to have occurred on the Caribbean coast of Mexico, although most reports for this area were negative (Table 17). Flagg in Hollings (1988) reported bleaching from Cozumel in 1987 but provided no further details. Roberts (1987) also listed Cozumel, but this was apparently taken from Hollings (1988) without citing the source (Roberts PC). The only other positive report we received was of mottled bleaching of *Siderastrea* spp. and other corals at Cozumel and the Yucatan Peninsula in January 1988 (Garrett PC) which seemed to describe hosts which were recovering from bleaching.

Periods when no bleaching occurred in particular geographic areas (Table 18) would also be very interesting to record. Bleaching in Australia is only known from one event in the mid-1970's (Table 18), 1980, 1982, 1983 (Oliver, 1985) and 1987. Since growth apparently ceases during bleaching (Reese et al., 1988), analysis of cores or sections of coral heads might indicate past bleaching events as reduced or unusual growth rings. Unfortunately, many other factors may cause unusual growth rings (Peters PC). However, Carriquiry et al. (1988) suggest both magnitude and chronology of ENSO events can be inferred from coral cores. Such studies might allow a more complete history of these events and a better understanding of the significance of present bleaching.

Table 17: Areas Noted Not Bleached During the 1987-1988 Events.

| LOCATION | DATES | SOURCE |
|---|---|---|
| Puerto Morales, Mexico | 1987 through April 1988 | Jordan-D. PC |
| Quintanaroo and Cozumel areas, Mexico | 1987 through May 1988 | Liddell PC |
| Campeche Bank, Mexico | 1987-May 1988[1] | Martinez PC |
| West Caicos, Turks & Caicos | July 1987 | Lott PC |
| Caribbean coast, Panama | Through November 1987 | Jaap in Hollings 1988 |
| Panama and Costa Rica[2] | 1987 | Glynn 1988b |
| Samoa, Palao, Guam | January to June 1988 | Birkland PC |
| Kenya[3] | 1988 | McClanahan PC[4] |
| Ryukyu Islands (except Okinawa) | 1988 | Muzik PC[5] |
| (also Ishigaki Island, Japan | 1980[6] | Kawaguti et al. 1981) |
| American Samoa | closely monitored since 1977[7] | Kluge-E. PC |

[1] Monthly examinations. [2] Pacific coasts. [3] Although bleached in 1987. [4] Monitored the areas that bleached in 1987 closely. [5] Called scientists and contacts on other islands. [6] When Okinawa and adjacent islands bleached. [7] 40 transects examined each year for *Acanthaster planci* damage.

Table 18: Periods With No Bleaching Prior to the 1987-1988 Events.

| LOCATION | TIME PERIOD | SOURCE |
|---|---|---|
| Indian Ocean | Never previously[1] | Wood 1988 |
| Tortola, BVI | 6 years prior | Keil PC |
| Easter Island[2] | From before 1930 to mid-1980 | Cea-E. & DiSalvo 1982 |
| Australia | Before mid-1970's | Bloomfield in Oliver 1985 |

[1] However, Guillaume et al. (1983), Faure et al. (1983, 1984) and Glynn (1983. 1984) reported bleaching in the western Indian Ocean.

[2] Unfortunately, we do not know if bleaching occurred there in 1982-83 or 1987-88.

## MORTALITIES

Deaths of stony corals, gorgonians and sponges were reported from many areas in the most intensely bleached region in the Atlantic in 1987-88 and some deaths of hosts occurred in almost all areas where bleaching was reported (Williams and Bunkley-W., 1989). Numbers of hosts killed in the Atlantic are being compiled from transect data by Lang (1988b) and will not be duplicated here. Tissue loss was reported most commonly in *Montastrea annularis* followed by *Agaricia* spp. in the greater Caribbean region. However, *M. annularis* was rarely and *Agaricia* spp. were frequently completely killed. At Cane Bay, St. Croix, 40% of *Diploria labyrinthiformes* were bleached and many were dead, while only 15% of *D. strigosa* were affected and smaller areas of each colony remained bleached (Gladfelter PC), an interesting difference between these 2 congeneric species.

Early reports of the 1987-88 coral reef bleaching event listed only zooxanthellate hosts as affected (Williams et al., 1987; Williams, L. and Williams, 1987; Williams, E. and Williams, 1988a). Glynn (1988b) suggested that a difference between the 1982-83 and 1987-88 bleaching events was that damage and mortalities in 1987-88 were restricted to photosymbiotic hosts while in 1982-83, damage and mortality included many non-photosymbiotic animals as well. The number of reports of deaths of non-photosymbiotic animals during the 1987-88 event (Table 20) is still very low, and the vast majority of the organisms affected appear to have been coral reef zooxanthellate hosts.

Table 19: Hosts Dead, Partially Dead (marked), or with Tissue Loss (marked "TL") During the 1987-1988 Event.

| SPECIES | LOCATION | DATE | SOURCE |
|---|---|---|---|
| *Acropora cervicornis*[1] | Bahamas | 1987 | Lang in Hollings 1988 |
| *Acropora palmata*[1] | Florida Keys (shallow) | 1987 | Jaap 1988[2] |
| *Acropora* spp.[1] | Colombia | 1987 | Lang 1988a,c |
| | Fiji | 1988 | Beckman PC |
| *Agaricia agaricites* (50-100%) | Mangrove areas, Puerto Rico | 1986, 1988 | Perez-T. PC |
| *Agaricia lamarcki* | San Salvador, Bahamas (below 25 m) | March 1988 | Hardy PC |
| *Agaricia* spp. (20%) | San Salvador, Bahamas (below 20 m) | Fall 1987 | Hardy PC |
| (20%) | Great Inagua, Bahamas (below 20 m) | Fall 1987 | Hardy PC |
| | St. Croix | by March 1988 | Gladfelter PC |
| | Turks and Caicos | Dec. 1987 - May 1988 | Lott PC |
| | Lee Stocking Island, Bahamas | Jan.-late March 1988 | Muscato PC |
| | Panama | 1987 | Lang 1988a,c |
| *Diploria labyrinthiformes* | Jamaica | by May 1988 | Woodley PC |
| | St. Croix | by March 1988 | Gladfelter PC |
| *D. strigosa* (some) | Buck Island, St. Croix | second bout | Hillis PC |
| *Diploria* spp. (TL)[3] | St. Croix | by March 1988 | Gladfelter PC |
| (some) | Lee Stocking Island, Bahamas | after Feb. 1988 | Muscato PC |
| *Eusmilia fastigiata* | Montego Bay, Jamaica | last few years | Smit-V. PC |
| *Millepora complanata* | Florida Keys (shallow) | 1987 | Jaap 1988[2] |
| *Millepora* spp. | South Florida | 1987 | Lang 1988a,c |
| *Montastrea annularis*(TL) | Florida Keys | 1987 | Hudson 1988 |
| (TL) | Puerto Rico | 1987 | Goenaga et al. 1988 |
| | Jamaica | by May 1988 | Woodley PC |
| (TL)[3] | St. Croix | by March 1988 | Gladfelter PC |
| (some) | Lee Stocking Island, Bahamas | late March 1988 | Muscato PC |
| *Montastrea cavernosa* | San Salvador, Bahamas (below 25 m) | March 1988 | Hardy PC |
| *Porites* sp. | Lee Stocking Island, Bahamas | after 1987 | Lang PC |
| *Porites* spp. | San Salvador, Bahamas (below 25 m) | March 1988 | Hardy PC |
| *Porites astreoides* | Jamaica | by May 1988 | Woodley PC |
| All corals (20%) | San Salvador, Bahamas (below 25 m) | March 1988 | Hardy PC |
| Anemones, some | Maldives | 1987 | Wood 1988 |
| Corals (a few) | Buck Island, St. Croix | first bout | Hillis PC |
| Corals with dead encrusted areas | Turks & Caicos | Spring 1988 | Lott PC |
| Corals (some) | Curaçao | 1987 | Sybesma 1988 |
| Corals (partial mortalities) | St. Lucia | 1988 | Lang PC |
| Corals (partial mortalities) | Florida Keys | Mid-July 1987 | Causey PC |

| | | | |
|---|---|---|---|
| Coral mortality | Mona Island, PR (30-40 m) | 1987 | Nieves PC |
| Most stony corals[4] | Maldives | 1987 | Wood 1988 |
| Most shallow corals | Fiji | Jan.-Feb. 1988 | Beckman PC |
| No significant mortalities | Saba, Netherland Antilles | up to July 1988 | Hof PC |
| Minimum mortalities | Gulf of California | 1987 | Reyes-B. PC |
| No mortalities | Cocos Island | 1987 | Glynn 1988b |
| No mortalities | Galapagos Islands | 1987 | Glynn 1988b |
| Soft corals (90%) | Kenya | 1987 | McClanahan PC |
| Stony corals (20-30%) | Kenya | 1987 | McClanahan PC |
| Stony corals (many) | Okinawa | 1988 | Muzik PC |
| Soft corals (many) | Okinawa | 1988 | Muzik PC |
| Overall damage to reef light | Okinawa | 1988 | Sakai PC |
| Numerous coral deaths | Reunion Island | 1987 | Faure PC |
| Few mortalities | Hawaii, Maui, Oahu (Hawaiian Islands) | 1986, 1987 | Choquette PC |
| Many parts of corals dead | St. John, U.S.V.I. | mid-July 1988 | Rogers PC |

[1] Possibly part of white band disease epizootic (?) or decline of *Acropora* spp. in Atlantic.
[2] Jaap in Hollings (1988) found no major mortalities in beginning, but later noted these.
[3] 30-50% of colonies. [4] Stony corals that bleached subsequently died.

Glynn, Perez, and Gilchrist (1985) demonstrated that coral symbiotic crabs in bleached or dead corals possessed fewer egg-carrying females, a higher emigration rate, a slight increase in mortality, and a decline in defensive behavior. They suggested that crabs in bleached corals had been deprived of their food. Invertebrates associated with corals in the Gulf of California became reduced in numbers on coral heads bleached in 1987 and abandoned dead corals entirely (Reyes-B. PC).

Glynn (1988b) reported that some species of corals disappeared from the reefs of Panama, and 2 species of hydrocorals may have suffered extirpation in the eastern Pacific region during the 1982-1983 coral reef bleaching. Some alcyonarians shrank to 1/3 of their original size during the bleaching in Okinawa in 1980 (Yamazato, 1981). Many soft-bodied cnidarians probably contracted or retracted and died unnoticed during the 1987-1988 bleaching events. Many of these hosts may have disappeared before the mortalities could be documented (Table 21).

The decline of *Acropora* spp. in the Atlantic (Table 21) occurred before and during the 1987 bleaching event. We did not monitor this decline in Puerto Rico, but in 1984 we participated in a census of damselfish gardens on a portion of Mario Reef, La Parguera, Puerto Rico, and in 1988 this study was repeated. Most of the lawns were in colonies of *A. cervicornis* in 1984, but in 1988 most were in other corals because of the scarcity of colonies of *A. cervicornis*.

Coral heads with dead tops are common on coral reefs in many areas. This damage is usually blamed on low water exposure, although this pattern is also seen on heads found below lowest water levels. Bleaching also seems to affect the top of coral heads more severely in many cases. In some cases only the upper surfaces bleached or these surfaces bleached more severely; or in the case of uniform bleaching, the upper surface often recovered more slowly, leaving a lighter colored cap long after the remainder of the colony regained normal appearance. Often the tops of coral heads die, while the rest of the colony recovers. Besides in Puerto Rico, *Montastrea annularis* with sloughed tissue on upper surfaces was noted in the Florida Keys (Hudson, 1988) and in Haiti (Goenaga and Vicente PC). Possibly, this commonly observed pattern of colony damage is caused by bleaching.

Robinson (1985) noted the loss of many 100-year-old coral colonies in the Galápagos in 1983. Shinn (1989) and Goenaga et al. (1989) have seen similar losses more recently in Florida and Puerto Rico. Death of these large massive corals is a reason for concern, but the changes that caused their demise may be even more important. Wood (1988) suspects reefs in the Maldive Islands have been so damaged, eroded and overgrown, that stony corals may not be able to recolonize. Lapointe (1989) forsees algal reefs replacing coral reefs in the Caribbean as a direct result of increased nutrification.

Table 20: Bleaching, Death, or Abnormal Behavior in Non-zooxanthellate (N) Hosts, and Non-photosymbiotic Animals.

| SPECIES | AFFECT | LOCATION | DATE | SOURCE |
|---|---|---|---|---|
| Bryozoan colonies | Mortalities | Gulf of California | 1987 | Reyes-B. PC |
| *Chama* sp. | Mortalities | Okinawa | 1986 | Tsuchiya et al. 1987 |
| Coralline Algae | Mortalities | Okinawa | 1988 | Muzik PC |
| Echinoderms (inshore) | Unusual behavior[1] | Florida Keys | 1987 | Jaap 1988 |
| *Echinometra mathaei* | Mass Mortality[2] | Okinawa | 1986 | Tsuchiya et al. 1987 |
| Mollusks (inshore) | Unusual behavior[1] | Florida Keys | 1987 | Jaap 1988 |
| Mollusks | Mortalities | Florida Keys | 1987 | Causey PC |
| Polychaetes(inshore) | Unusual behavior[1] | Florida Keys | 1987 | Jaap 1988 |
| *Revitrona caputserpentis* | Mortalities | Okinawa | 1986 | Tsuchiya et al. 1987 |
| *Stichopus* sp. | Mortalities | Kenya | 1987 | McClanahan PC |
| *Strombus gigas* | Mortalities | Florida Keys | 1987 | Berg in Jaap 1988 |
| *Stylaster roseus* | Bleaching | Mona Island, Puerto Rico | 1987 | Kontos PC |
| | Mortalities | Mona Island | 1989[4] | This paper |
| Tunicates | Mortalities | Okinawa | 1988 | Muzik PC |
| Urchins | Mortalities (hyperthermia) | Okinawa[3] | 1987 | Tsuchiya et al. 1987 |
| *Xestospongia muta*(N) | Bleaching | Caribbean | 1987 | Williams & Bunkley-W. 1989 |
| Other encrusting organisms | Mortalities | Okinawa | 1988 | Muzik PC |
| Other shallow-water animals | Mortalities | Florida Keys | 1987 | Causey PC |
| Other sponges(N) | Bleaching & mortalities | Caribbean | 1987 | Williams & Bunkley-W. 1989 |

[1] And lethargy probably due to hyperthermia. [2] Accompanied by the bleaching and death of hermatypic corals. [3] But no bleaching was noted in 1987 (Sakai PC). [4] Noted.

Table 21: Disappearance or Decline of Coral Reef Hosts.

| SPECIES | OCCURRENCE | LOCATION | DATE | SOURCE |
|---|---|---|---|---|
| *Acropora cervicornis* | Die-off | Caribbean | 1987[1] | This paper |
| | Die-off | Bahamas | 1987 | Lang 1988a,c |
| *Acropora palmata* | Die-off | Caribbean | 1987[1] | This paper |
| Many anemones | shrank drastically and apparently died | Caribbean | 1987 | This paper |
| Many hosts[2] | Disappeared | Florida Keys | 1987 | Causey PC |
| Some hosts | Disappeared | Kenya | 1987 | McClanahan PC |
| Sponges[3] | Extirpation | Caribbean | 1987[1] | Vicente 1989 |
| *Ricordia florida*[2,4] | Disappeared | Florida Keys | 1987 | Causey PC |

[1] Prior to. [2] Formerly common. [3] Several species. [4] Reported bleached in the Bahamas and Puerto Rico, but not in the Florida Keys or Florida (Williams and Bunkley-W. 1989).

## RECOVERY

Jaap (1988) and Jaap in Hollings (1988) suggested that the density of zooxanthellae in a colony can recover from short-duration bleaching in 6-8 weeks. Hoegh-G. and Smith (1988a) found recovery from 50% loss of zooxanthellae, caused by a 4 hour exposure to 32°C, occurred over 23 days. Gladfelter (1988) suggested that short-term-bleached hosts will recover, but those suffering long-term-bleaching will die. Bleaching in 33 sites over 6 years along the Red Sea coast was found to be a short-term phenomenon of the warm, rainy season (Antonius, 1988). Bleached hosts at Guam, a few years ago, recovered in a few weeks (Birkland PC).

Table 22: Rates or Patterns of Recovery.

| SPECIES | RECOVERED | LOCATION | DATE | SOURCE |
|---|---|---|---|---|
| **RATE** | | | | |
| *Tridacna* spp. | 24-48 hrs | Bonaire | 1987 | Lott PC |
| *Eunicia* spp.[1] | quickly | Turks and Caicos | 1987 | Lott PC |
| *Millepora* spp. | first | Caribbean | 1987 | Williams & Bunkley-W. 1989 |
| | quickly | Turks and Caicos[1] | 1987 | Lott PC |
| Shallow corals | quickly | Turks and Caicos | 1987 | Lott PC |
| Corals | 4-6 weeks | Cocos Island | 1987 | Glynn 1988b |
| | 4-6 weeks | Galápagos | 1987 | Glynn 1988b |
| *Agaricia* spp. (deep) | last | Caribbean | 1987-1988 | Williams & Bunkley-W. 1989 |
| | slowest | Cayman Islands | 1987 | Byrnes PC |
| Deeper corals | little | Florida Keys | May 1988 | Causey PC |
| | last | Caribbean | 1987-1988 | Williams & Bunkley-W. 1989 |
| | last | Turks and Caicos | 1987 | Lott PC |
| **AMOUNT OF RECOVERY** | | | | |
| Anemones | some | Maldives | after Dec. 1987 | Wood 1988 |
| Hosts | some | Turks and Caicos | Spring 1988 | Lott PC |
| Hosts | 1/4 colonies still bleached | Puerto Rico | May 1988 | Goenaga et al. 1988 |
| *Agaricia agaricites* | 90%[2] | South Florida | 1987 | Ferrer PC |
| *Montastrea annularis* | 90%[2] | South Florida | 1987 | Ferrer PC |
| *Siderastrea siderea* | 90%[2] | South Florida | 1987 | Ferrer PC |
| Shallow corals | most | St. Croix, USVI | Jan. 1989 | Tobias PC |
| Corals | largely | St. John, USVI | Mid-July 1988 | Rogers PC |
| Hosts | well advanced | Lee Stocking Island, Bahamas | June 1988 | Lang PC |
| Hosts | Steadily | Jamaica | Dec. 1987-May 1988 | McFarlane & Goreau 1988 |
| **NO RECOVERY, CONTINUED BLEACHING** | | | | |
| Hosts | –[3] | Maldives | Dec. 1987 | Wood 1988 |
| Stony corals | – | Maldives | after Dec. 1987 | Wood 1988 |
| Stony corals, gorgonians | –[4] | Puerto Rico | March 1988 | Morelock PC |
| Stony corals | – | Little Cayman, Cayman Islands | March 1988 | Sefton PC |

| | | | | |
|---|---|---|---|---|
| *Agaricia* spp. | – | Little Cayman, Cayman Islands | March 1988 | Sefton PC |
| Deep reefs | – | Florida Keys | March 1988 | Lang PC |
| | – | St. John | Mid-March 1988 | Hardy PC |
| | – | Antigua | Mid-March 1988 | Hardy PC |
| | – | Mona Island | Mid-March 1988 | Hardy PC |
| *Agaricia lamarcki* | – | Jamaica | May 1988 | Woodley PC |
| Hosts | – | San Salvador, Bahamas | May 1988 | Gerace PC |
| **BEGINNING OF RECOVERY** | | Florida Keys | Mid-Nov. 1987 | Causey 1988, Jaap 1988 |
| | | Gulf of California | late Nov. 1987 | Reyes-B. PC |
| | | South Florida | After Nov. 1987 | Causey 1988, Jaap 1988 |
| | | Western Colombia | Dec. 1987 | Bohorquez 1988 |
| | | St. Croix[5] | Mid-Dec. 1987 | Hillis PC |
| **FULLY RECOVERED SHALLOW REEFS** | | | | |
| | | Puerto Rico | Mid-March 1988 | Hardy PC |
| | | Antigua | Mid-March 1988 | Hardy PC |
| | | Mona Island | Mid-March 1988 | Hardy PC |
| | | Florida Keys | March 1988 | Lang PC |
| | | Jamaica | May 1988 | Woodley PC |

[1]Bleached first. [2]100% bleached on 25 Sept. recovered to 10% bleached on 7 Dec. 1987.
[3]Widespread bleaching. [4]Photograph taken by Morelock PC. [5]But also new bleaching.

Hudson (1988) noted splotched patterns of coloration in recovering corals in the Florida Keys, and Newton (PC) reported bicolor patterns in recovering corals in Bonaire. The various color patterns and shades of recovering colors were similar to the ones found in the beginning of the bleaching process, and to those of partially bleached corals. Only by following individual corals, can recovery be differentiated from new bleaching or partial bleaching.

Glynn and D'Croz (1989) histologically demonstrated that corals in the eastern Pacific had not completely recovered from bleaching 2 years after the 1983 event. Suharsono (1988) found that the reefs damaged by bleaching in Indonesia in 1983 had not completely recovered in 4 years.

Following the 1987-88 coral reef bleaching events and despite continuing occurrence of disease in many coral species, Bythall (1989) found "encouraging signs of substantial levels of recruitment in many areas" at Buck Island, St. Croix, USVI. This was part of a long-term monitoring program on the reef at Buck Island. Yoshioka and Buchanan (PC) also noted coral recruitment following the 1987-88 bleaching on their long-term study area off southwestern Puerto Rico. We also noted recruitment in areas damaged by the bleaching at Mona Island, southwestern Puerto Rico and St. Thomas, USVI, while at the same time, finding what appear to be increased levels of BBD and continuing WBD.

## VARIATION AND COMPARISONS

The description of bleaching in the Caribbean in 1987-88 (Williams and Bunkley-W., 1989) could be best characterized as showing high variation. Few if any trends can be assembled which are not contradicted by some reports. The patterns and extent of bleaching seem to suggest a large number of local, unrelated, practically unique events but they are too highly coordinated to be coincidental. Lang (1987; 1988a,c) and Lang in Hollings (1988) noted high variability among species, locations, habitats, patterns and extent of bleaching in the Bahamas and Colombia, Losada (1988) found similar variation in bleaching in Venezuela, Oliver (PC) in Australia and many of our reports from the Caribbean commented on this variation. Some hosts bleached in only 1 or a few locations in the Caribbean (Williams and Bunkley-W., 1989). Hof (PC) found *Cliona aprica* bleached in Saba, Netherland Antilles, although Vicente (PC) could not find even partially bleached specimens among the sponges he monitored in Puerto Rico. Losada (1988) found *Briarium asbestinum* commonly bleached in Venezuela, while it was rarely bleached in Puerto Rico, and was only reported to bleach in 3 of 35 locations in the Caribbean (Williams and Bunkley-W., 1989). Sandeman (1988b) found *Montastrea cavernosa* more intensely and more often bleached than *M. annularis* in Jamaica, and Losada (1988) found the same situation in Venezuela. However, most other reports suggested *M. annularis* bleached both more frequently and more intensely than *M. cavernosa*. Woodley (1988) suggested that *M. cavernosa* did not bleach in Jamaica.

Hardy (PC) examined 11 widespread sites in the Bahamas, British Virgin Islands, Saba and Mona Island during the 1987-88 bleaching event. He found San Salvador, Bahamas, to be the most severely bleached area. Bleaching at Key West in 1987 was not as severe as at Looe Key, but in 1983, bleaching had been much worse at Key West than at Looe Key (Jaap, 1988; Jaap in Hollings, 1988). In Colombia, Bohorquez (1988) found bleaching at Islas del Rosario and San Bernardo Archipeligo extensive and similar, but noted less bleaching at Tyrona Park. In the Turks and Caicos, less bleaching occurred on Grand Turk and Providenciales, South Caicos (Lott PC).

In Australia, the 1987 event was similar to the 1982-83 event in timing and species most severely affected (Oliver PC). Bleaching in Florida was more extensive in 1987 than in 1983 or 1973 (Causey, 1988). The 1987-88 events were the most massive known in Florida, exceeding all previous in geographic extent, bathymetry, and longevity (Jaap, 1988). The 1987 event in the western Caribbean coast of Colombia (Lang, 1987; Sanchez-R. and Gomez-R., 1987) was judged in the beginning to be less severe than in 1983 (Lang in Hollings, 1988). Glynn (1988a,b) compared the bleaching in the eastern Pacific in 1983 and the Caribbean in 1987 and found that in 1983 smaller areas were severely affected, branching rather than massive corals were most affected, and non-zooxanthellates were affected. The affected area in the Caribbean was at least twice as large as the areas in the eastern Pacific (Glynn, 1988b), also the area bleached in 1987 in Australia was at least twice the size of areas bleached there in 1982-83, and could be 3-4 times the size if the north coast was involved. Many branching corals were affected in the Caribbean in 1987, and mortalities were higher in branching species in some areas than in massives (although WBD may also be involved). Some non-photosymbiotic animals died during the 1987 event but many more died during the 1983 event in the eastern Pacific. Overall, the 1987-88 event was the most severe, extensive and long-term bleaching ever recorded.

## PREVIOUSLY UNREPORTED BLEACHING EVENTS AND COMPARISON TO KNOWN REPORTS

Part of the problem of understanding bleaching events is that the information is patchy and incomplete. In many areas no coral reef scientists are available to make observations. Even when observations were recorded in the past, no "clearing house" for such information was available. Fortunately, in seeking information about the 1987-88 events, some new historic information surfaced. More reports of past bleaching are vital for understanding the patterns and causes of these events.

### 1969

An intensive and extensive bleaching event occurred on coral reefs of southwestern Puerto Rico in 1969 (Almodovar PC, Atwood PC). The bleaching was probably caused by 38.1 cm of rain during a hurricane that preceded the bleaching (Almodovar PC).

### 1979-80

In June 1979, an extensive and long-term bleaching event began on Bonaire (Hof PC). It developed progressively and became most extensive and intense in September and October, 1979. The event ended in February 1980. Bleaching occurred on all but the windward coast of the island from 10-40 m depth. Bleaching began in the knobby, columnar form of *Montastrea annularis*. Later it affected other growth forms of *M. annularis* and *M. cavernosa*, *Agaricia lamarcki*, *Colpophyllia natans*, and *Siderastrea* spp. Quantitative transects 90 X 4 m were run 10 September 1979. A transect at 10-15 m depth contained 37 colonies of *M. annularis* bleached, and another at 15-18 m, had 94 colonies bleached. Few if any dead corals were noted during or after the event (Hof PC).

Goenaga and Canals (1979) reported bleaching of *Millepora complanata* in a small area of Puerto Rico in 1979. This damage was apparently caused by lowered salinity and probably was not related to the large scale event in Bonaire.

In the summer of 1980, coral reef bleaching occurred in several areas in the Florida Keys. A massive fish kill which would later spread throughout the Caribbean (Williams, E. and Williams, 1987) was occurring at the same time. The calm, doldrum weather conditions prior to this bleaching event were similar to those preceding the 1973, 1983, and 1987 events in the Florida Keys (Causey PC).

Upton and Peters (1986) found partially bleached, mottled bleached, patchy bleached or bleached specimens with necrosis, of *Agaricia agaricites* in Puerto Rico and Jamaica, *Montastrea cavernosa* and *Meandrina meandtites* in Puerto Rico. Most of these affected specimens were infected with a coccidian that caused the bleaching. Some bleached specimens, however, were not infected. All were collected in the warmest-water period of the year (August-September, 1980) in a year when bleaching occurred in several other widely separated locations.

Bell and Galzin (1988) noted that much of the coral in the lagoon at Mataiva Atoll, died in late 1980, but did not explain why.

## 1981

Some bleaching of hard corals occurred on the reefs of western and southwestern Puerto Rico in August 1981 (Williams et al., 1987; Vicente PC). A sea surface temperature positive anomaly occurred at this time (temperatures at the shelf break >29°C) and was comparable to a similar one in 1987 (Atwood et al., 1988). Specimens of *Diploria strigosa* and *Porites astreoides* sampled in August 1981 were infected with a coccidian which was capable of causing minor patchy bleaching in other corals (see above) (Upton and Peters, 1986).

## 1983

Soekarno (PC) found 72 species in 33 genera of scleractinian corals, *Millepora platyphylla*, *M. dichotoma* and some soft corals and sponges bleached on coral reefs of the Seribu Islands (off Jakarta, Indonesia) and the Kaimun Java Islands (off central Java), Java Sea, from March to May 1983. Bleaching began suddenly and affected 40-50% of the corals from the surface to 15 m. The entire surfaces of affected hosts were bleached. Mortalities occurred in 10-15% of the bleached corals with 80-90% of the deaths occurring in mid-May. Not all individuals of each species of host bleached or died in each habitat or depth. Recovery of the surviving hosts began by late July. Bleaching and mortalities were associated with high seawater temperatures. Suharsono in Glynn (1984a) noted, in less detail, what was presumably the same event. Suharsono (1988) has monitored the coral reefs at Pulau Pari, Pulau Seribu (Indonesia) since 1979. In April 1983, seawater temperatures (normal maximum 28°C ±2°C) remained at 33°C for 3 months. Coral cover was drastically reduced by the bleaching.

Bleaching of *Acropora* spp. occurred in the inner shoreline of the southwestern lagoon of New Caledonia in 1983 (Thomassin PC).

## 1986

Extensive coral reef bleaching of *Pocillopora* spp. began in August 1986 on the Hawaiian islands of Hawaii, Maui, and Oahu from the shoreline to 45.7 m depth. From 20-100% of the surface area of approximately 80% of the colonies were bleached. Bleaching developed progressively over 3-4 months and became most intense in early November. Bleaching seemed to begin about the same time on each island and in all habitats. Water temperatures may have been slightly above normal. Corals recovered with little or no mortality by the end of December. Bleaching started at the tips of colonies and worked its way basally. Selected colonies were tagged and photographed periodically and a 48.3 km section of the coast of Hawaii was examined during the event. Previous bleaching events have not been noted in the Hawaiian Islands (Choquette PC). Three photographs taken during this event by Choquette (PC) seem to be *Pocillopora meandrina*, *P. verrucosa*, *Millepora* sp. and *Porites* sp. In October 1986 on the south coast of the Hawaiian island of Maui, *Pocillopora meandrina*, *P. damicornis*, *Montipora* sp. and *Porites lobata* were bleached from 0.6-10.7 m depth. *P. meandrina* was the most intensly bleached. In November 1986, reports were received of dying corals in the Napili and Kapalna area. Ninety percent of *Montipora* sp. were bleached, but no *Pocillopora* sp. Reports were also received about bleaching on the island of Hawaii at that time. Calm weather conditions and warm water temperatures occurred during this event (Hau PC).

In May 1986, massive coral reef bleaching and high mortalities occurred on the coral reefs of Mayotte Island (Mozambique Channel) which closely resembled the event there in 1983 (Thomassin PC). The 1983 bleaching event was described by Faure et al. (1983, 1984).

Tsuchiya et al. (1987) found bleaching of coral reef hosts during a mass mortality of urchins in the southern part of Okinawa and on several adjacent small islands in June 1986. Reef hosts in northern Okinawa did not bleach at this time (loc. cit., Sakai PC).

In November 1986, *Agaricia agaricites*, *Stoichactis helianthus* and *Favia fragum* bleached in the mangroves of southwestern Puerto Rico. Approximately half of the colonies of *A. agaricites* bleached over 80-100% of their surfaces. Only 5-10% of the *F. fragum* were affected. Bleaching was slightly more intense in the more shallow and more light-exposed colonies. The onset of bleaching was sudden, and the most intense bleaching occurred in November and December 1986. In some areas half of the *A. agaricites* colonies died. Recovery of the remainder was complete in January of 1987 (Perez-T. PC). This event occurred at the same time of the year as bout #2 in the 1987 events (Table 15).

Also in November 1986, most of the *Millepora* spp., many stony corals and a few gorgonians and sponges bleached in Culebra Island off eastern Puerto Rico. The event seemed to have become intense and widespread suddenly in November, but may have actually started as early as September 1986. *Acropora cervicornis* was the first coral to bleach at depths between 9.1-15.2 m. Later, *Diploria strigosa* and other hosts bleached between 4.6-22.9 m. *Millepora* spp. became totally bleached, most hard corals bleached everywhere except their bases. *Agaricia* spp. bleached along the edges of the colony. Many of the most severely bleached colonies died. Water temperatures may have been a little higher than usual (Perkins PC). Mignucci-G. (PC) also noted bleaching and mortalities of *Acropora palmata* and other corals at Culebra in 1986.

A 2 m high, 3 m diameter colony of *Dendrogyra cylindratus* was completely bleached on the bank reef off Barbados in mid-July 1986. A week later it began to turn brown around the base, 2 weeks later about 25% of the colony had recovered, in 3 weeks the entire colony was a normal color. Some time during the last week of this process, a similar colony 20 m away totally bleached. In 4 weeks the color recovered in the second colony. Twenty neighboring colonies within an approximately 2,500 m radius retained their normal colors. Environmental conditions seemed to be normal during this time (Tomascik PC). This coral was one of the most resistant hosts to bleaching and was never reported totally bleached during the 1987-88 events. Smit-V. (PC) also noted this coral to bleach and recover recently, but prior to the 1987 event, in Jamaica.

Large areas of *Acropora cervicornis* died in the fall (warm water period) of 1986 off San Salvador, Bahamas (Hardy PC). Whether this was due to the 1986 bleaching event or to the WBD epizootic is not known.

## UNKNOWN RECENT DATES

Massive bleaching of *Acropora* spp. occurred at Amami Island and Tokuno Island, Amami Islands, Japan, sometime before 1987. It was probably caused by unusually heavy rains coinciding with extremely low (negative) tides as in 1988 in Okinawa (Muzik PC). Bleaching occurred in large patches of corals several years ago in Guam (Birkland PC).

# POTENTIAL CAUSES OF THE 1987-88 EVENT

## DISEASE

Bacteria (Glynn et al., 1985), a coccidian (Upton and Peters, 1986), fungi (Jaap, 1988, Te Strake et al., 1988), and a ciliate (Nunn PC) have been isolated from bleached corals. The ciliate was only abundant in 1 case and was possibly only associated on necrotic tissue as frequently occurs (Peters, 1984). A perkinsid parasite was found in bleached and/or dying giant clams (Goggin and Lester, 1988; Braley PC, Goggin PC). White band disease (WBD) and black band disease (BBD) were noted in corals bleached in the 1987-88 event. None of these diseases appears to cause major bleaching events. Physical stresses triggering an infectious disease was suggested as a possible cause of bleaching (Williams et al., 1987). Ruetzler (1988) documented a sponge's photosymbionts (cyanobacteria) becoming pathogens under environmental extremes (such as high water temperatures) and suggested that this is what also happens in BBD. Circumstantial evidence suggests that a parasite in combination with hypothermia killed 36% of the giant clams on some Australian coral reefs (Goggin and Lester, 1988). Onset of bleaching in multiple, widely separated locations was said to preclude the possibility of disease (D'Elia in Roberts, 1987; Jaap, 1988). Many potential pathogens are normally associated with hosts and may not cause disease until hosts are stressed. Spread from a single point of origin, such as in the *Diadema antillarum* mass mortality (Lessios et al., 1984) is an exceptional pattern often found in new diseases (Williams, E. and Williams, 1987). The presence of partially affected and non-affected hosts mixed with bleached ones, might also suggest a pathogen, (Williams et al., 1987) as well as the erratic and multiple bouts of the 1982-83 and 1986-89 events. Failure to transmit a disease condition from bleached grafts to unbleached hosts (Glynn et al., 1985) does not eliminate infectious disease as a possibility. The grafting experiment (loc. cit.) would have exposed a primary pathogen, but the observed bleaching and deaths were more likely caused by a secondary pathogen dependent upon some major degradation of each host's defenses. For the grafts to express a secondary pathogen, a new high temperature bout would be necessary after the grafts were in place. An examination of these grafted colonies after the 1987 event might be instructive.

Williams et al. (1987) suggest that a single disease of the diverse species and phyla of hosts affected was unlikely, but a disease of the more similar photosymbiotic zooxanthellae might be a possibility. However, the addition of hosts with cyanobacteria and non-photosymbiotic animals to the bleaching list (Williams and Bunkley-W., 1989 and present paper) makes the suggestion of a disease of the zooxanthellae less likely.

## LIGHT EFFECTS

Fisk and Done (1985) suggested that increased solar radiation with possible unidentified synergistic stresses caused the 1982 bleaching in Australia. Harriott (1985) also suspected radiation as the primary cause, because most bleaching occurred on the upper and unshaded surfaces of colonies in shallow, clear water. However, she (loc. cit.) did note that elevated seawater temperatures occurred, and Oliver (1985) suggested that elevated seawater temperatures were to blame. Light effects were suggested as a possible cause and/or intensifier of the 1987-1988 bleaching (Williams et al., 1987; Williams, L. and Williams, 1987, 1988; Sandeman, 1988a,b; Williams, E. and Williams, 1988a; Woodley, 1988). Evidence for light effects was based largely on bleaching being more pronounced in more exposed areas of effected hosts (loc. cit.). Greater bleaching on upper or more light exposed surfaces of stony corals, gorgonians and zooanthids and/or tissue loss on these surfaces (Hudson, 1988; Goenaga et al., 1988, 1989; Bunkley-W. et al., 1989) was noted in almost all of the reports we received. Gorgonians were sometimes striped white above and below the plane of most direct light (Williams, L. and Williams, 1988). Portions of upper surfaces which fell in shadows of fixed objects were often not bleached (Williams and Lang, 1988). This seems to be one of the few non-contradictory elements in our otherwise highly variable data and seems to indicate a uniform effect of light on bleached hosts. Unfortunately, in some areas, reefs which bleached were obscured by suspended sediments or algae in the water column which precluded light effects during the event. In the Florida Keys, sediment laden waters present in the beginning of the event were replaced later by algal blooms. These effects obscured the reefs from light prior to and during the periods of most intense bleaching (Causey PC). The observed patterns on exposed surfaces there could not have been caused by light. Furthermore, this pattern does not necessarily indicate an increase in light effects. Corals experimentally bleached with increases of temperature, bleached more intensly on light exposed surfaces without any increase in light intensity (Jokiel and Coles, 1977). If the light levels are reduced 10 times, corals can withstand higher temperatures without shedding zooxanthellae (Hoegh-G. PC). This explains the "shading effect". Thus, light and shadow did affect the intensity of bleaching (Goenaga et al., 1988; Jaap, 1988; Jaap in Hollings, 1988; Sandeman, 1988b; and Woodley, 1988) but this is not evidence for increased levels of light as a cause of the bleaching. Microsurfaces of hosts in light are warmer than in the shade (Peters PC). Slight differences may be significant when ambient temperatures are near the levels necessary to cause bleaching.

Woodley (1988) suggested that bleaching of *Montastrea annularis* in Jamaica in depths shallower than 12 m, but not below, was an indication that bleaching was caused by light effects. The thermocline was at 50 m on these reefs, therefore, temperature caused bleaching should have been uniform to that depth (loc. cit.). Sandeman (1988b) found that no *M. annularis* bleached below 20 m in Jamaica. Assuming that the thermocline and temperature relationships were constant throughout the bleaching event in Jamaica (which has not been established), either synergistic light effects or some depth-related difference in this host caused the observed differences. Sandeman (1988b) suggested that differences in zooxanthellae in different colonies and even different parts of the same colony could explain the different patterns of bleaching. He (PC) found at least 7 different strains of zooxanthellae in *M. annularis* in Jamaica. Battey and Porter (1988) noted *M. annularis* occupies the largest depth distribution of any known photosymbiotic scleractinian coral. The unusual number of strains of zooxanthellae might somehow be related to the unusual depth distribution of this coral. If different strains either occur or predominate at different depths, then these zooxanthellae may allow the hosts to react differently. Other hosts bleached below 12 or 20 m in Jamaica, suggesting that some peculiarity of *M. annularis* was responsible for the observed depth pattern, not a lessening of synergistic light effects with depth. Lott (PC) also found deeper *M. annularis* did not bleach in the Turks and Caicos while *Agaricia* spp. at the same depths bleached.

Jaap in Hollings (1988) suggested that ultraviolet (UV) light does not penetrate well in sea water, and used this as an argument against light effects. He concluded that the bleaching to 70.1 m could not be caused by light. Woodley (1988) used the same assumption as an indicator of light effects. Jokiel (1980) suggested UV light penetrates seawater almost as well as visible light. Coral colonies held in an aquarium in St. Thomas under artificial light also bleached and died during the event (Nunn PC) indicating severe bleaching occurred in the absence of sunlight.

The recent decline in populations of *Chondrilla nucula* in Puerto Rico (Vicente, 1989) may be an indicator of light effects. Exposed sponges have become overgrown by filamentous algae while more protected specimens were not affected (loc. cit.). This sponge bleached during the 1987-88 event (Williams and Bunkley-W., 1989) and its decline could be related to this damage. Just as in the case of bleaching, it could also react negatively to the combination of increased temperatures and sunlight exposure.

The best evidence for light-related damage to bleached hosts is the reduced pigments in zooxanthellae remaining in bleached corals (previously discussed). Goenaga et al. (1988) suggest that exceptionally calm seas coupled with reduced water turbidity was a major factor in the mass expulsion of zooxanthellae in 1987-88. However, Hoegh-G. and Smith (1988a,b) suggest temperature increases, not light increases, cause the expulsion of zooxanthellae and that increased light reduces pigments in existing zooxanthellae. We believe that light effects can damage coral reef hosts when the period of the year with the most direct solar radiation coincides with a long period of abnormally calm, clear weather. Moving corals to a more shallow position on a reef can cause bleaching, presumably because of increased levels of light (Acevedo and Goenaga, 1986; Sandeman, 1988b). Greater water clarity from a gradual reduction of suspended material, and less diffusion at the surface in extremely calm seas, might similarly increase the amount and intensity of light received by corals. Some damage and synergistic effect of light probably occurred during the 1986, 1987-88, and 1989 bleaching, but increased seawater temperatures were most probably the primary cause.

## LOW TIDES

Sea level drops associated with El Niño Southern Oscillation (ENSO) events caused mass mortalities of reef-flat animals on Guam (Yamaguchi, 1975) prior to the 1982-83 event, on Moorea Island (south Pacific) and Nukunona Atoll (central Pacific) in 1983 (Glynn, 1984a), in French Polynesia (Salvat in Glynn, 1988) and probably again in Moorea in 1987 (Richmond PC). Low tides were involved in the Florida Keys' 1987 event (Causey, 1988), in bleaching and mortalities in 1988 in Fiji (Beckman PC), in mass mortalities and bleaching in Okinawa in 1986 (Tsuchiya et al., 1987), and extremely low tides 16-17 May 1988 in the Okinawa bleaching (Walker PC). Drastic sea level drops produce bleaching and extensive mortalities, moderate drops may intensify the effects of elevated temperatures and solar radiation.

## DOLDRUMS

Unusually calm days with little or no wind or sea movement were noted before and during the event in Puerto Rico, Florida (Causey, 1988; Hudson, 1988; Jaap, 1988; Shinn PC), Mona Island

(Kontos PC), Australia (Oliver PC, Zann PC) and in the Hawaiian Islands (Hau PC) in 1987 (and in 1986 - Choquette PC, Hau PC); and in Jamaica (Gates PC) and Florida (Causey PC) in 1988. Winds in the Bahamas may have been more from the south, southwest and west than usual (Lang in Hollings, 1988). The summer of 1987 was widely reported to be very calm with lower than usual trade winds (Williams and Lang, 1988). Such "doldrum" conditions often precede major marine ecological disturbances in the Florida Keys (Jaap in Hollings, 1988; Bohnsack PC; Causey PC). Tsuchiya et al. (1987) considered clear, calm weather an important factor in the 1986 hyperthermia mass mortalities and bleaching in Okinawa. These conditions favor local increases in temperature in inshore areas, poor circulation, and the formation of hypersaline waters (Williams and Lang, 1988) and would also favor greater water clarity from a gradual reduction of suspended material and less diffraction at the surface allowing greater penetration of light. The calm conditions in the Florida Keys allowed turbid waters from Florida Bay to remain over the reef before the event and an intense algal bloom to remain over the reefs during the event.

## HYPERSALINE WATER

Clear, calm days with high air temperatures may have allowed the development of unusually warm, hypersaline water in confined shallow areas in Florida (Jaap, 1988), the Bahamas (Lang et al., 1989) and possibly in the Maldives (Wood, 1988), Culebra Island (Tucker PC) and other limited areas, that intensified the bleaching process. The hypersaline water formed by this process sank and flowed over the shelf and down in parts of the Bahamas to intensify the bleaching of deeper hosts (to 55 m) (Lang et al., 1989), and may have intensified the bleaching around "inlets" and channels in the reef (Hudson, 1988; Jaap, 1988) and depressions and grooves in corals in Florida (Jaap, 1988) and possibly in other areas (Hardy PC). In the Bahamas, such "underflows" are known to flow daily at low tides for up to 5-6 months of the year (Lang et al., 1989). Particularly severe bleaching along both sides of the Wadu Channel in the Maldives (Wood, 1988) may have a similar cause as suggested for the sides of the channels in the Florida Keys.

## TURBID WATER

Turbidity may have complicated and intensified the 1987 bleaching in the Bahamas (Bland PC), Culebra Island (Perkins PC), Florida Keys (Causey, 1988), Andaman Islands (Wood PC), and Mayotte Island, Mozambique Channel (Faure PC). From 12 July to 18 September still, murky waters covered the Florida Key reefs (Causey PC). Warm, turbid waters covered the reefs at Isla del Rosario, Colombia, for at least 1 day in July 1987 (Lang in Hollings, 1988). In September 1987, warm, turbid waters covered the reefs in Santa Marta, Colombia (Zea PC). When bleaching was observed in St. Vincent and the Grenadines, the water on the reefs was turbid (Causey PC). From March through April 1987 in the Maldives, a notable increase in phytoplankton occurred (Wood, 1988). Visability during the bleaching in the Gulf of California was about half of the usual distance (Reyes-B. PC). These conditions could, and in many cases were noted to, contribute to the increase of inshore water temperatures.

## EL NIÑO SOUTHERN OSCILLATION

In the Florida Keys, where bleaching has been recorded more frequently than anywhere else, bleaching usually coincides with El Niño Southern Oscillation (ENSO) phenomenon (Scientific Committee on Ocean Research, 1983) of the eastern Pacific (Jaap, 1988; Causey PC). This could indicate that bleaching is associated with global atmospheric disturbances (Williams and Lang, 1988). The 2 most extensive world-wide coral reef bleaching complexes coincided with ENSO years (1982-83, 1986-88). Many physical effects associated with the last 2 ENSO events probably caused or increased bleaching on coral reefs. Three were prominent: (1) elevated seawater temperatures; (2) calm seas; and (3) lowered sea levels. Brown (1987) divided the 1982-83 bleaching events into ENSO-related and non-ENSO-related. ENSO disturbances are now considered to have global effects (Rasmusson and Wallace, 1983; Cane, 1986; Glynn, 1988b, 1989a); therefore, the Caribbean and Florida bleaching in 1983 which Brown (1987) listed as due to increased temperatures, may have been ENSO related. The 1982 event in Australia occurred before the 1982-83 ENSO began and most of the 1988 bouts (and 1989 bout) occurred after the 1986-88 ENSO ceased. The 1979-80 bleaching events also did not occur in years with an ENSO event [moderate or stronger ENSO as defined by Quinn et al. (1987) or by the Scientific Committee on Ocean Research (1983)]. The disturbances associated with ENSO events are very important in causing or intensifying coral reef bleaching, but bleaching is not simply an ENSO effect.

## DETERIORATION

The health of the world's oceans and especially coastal areas is, in general, declining (Jeftic et al., 1988). This is further documented by the increasing numbers of major marine ecological disturbances (Table 23). Sinderman (1988) noted that epizootic ulcerative syndromes in marine fishes world-wide is an indicator of the degradation in the coastal marine environment. He considers the world-wide distribution of coral reef deterioration associated with coral reef bleaching and mortalities to be an analogous example of this trend.

Coral reefs are deteriorating in the Pacific (Gomez, 1988) and the Atlantic (Rogers, 1985; Lang in Hollings, 1988) due to sedimentation, industrial or agricultural chemicals and sewage pollution and eutrophication. Of 103 countries with coral reefs, deterioration of reefs as a result of human activities was reported in 93; damage due to natural events (hurricane, cold temperatures, El Niño associated phenomena and coral predators) in 77 (Wells, 1988). Voss (1989) suggested that the world's coral reefs are deteriorating from unknown causes. In the last 5 years coral reef scientists all over the world have reported alarming incidences of coral reef destruction (Maizan, 1988). Best and Boekschoten (1988) found that opportunistic species which could adapt to the dynamic condition on coral reefs, including the influence of man, were beginning to dominate reefs world-wide. Jaap in Hollings (1988) suggested pollution or contamination may have had a synergistic effect in the 1987 bleaching. Rogers (1985) found many Western Atlantic coral reefs had significantly deteriorated in the last 10 years. Carpenter in Hollings (1988) suggested "all Caribbean reefs" were under "stress". Dahl (1985) found most accessible coral reefs in Polynesia were in various stages of decline. Muzik (1985) found severe and possibly irreversible deterioration of the coral reefs of the Ryukyu Archipeligo. Sudara and Nateekarnchanalap (1988) found coral reefs in the Gulf of Thailand and in the Andaman Sea showed degradation. Hutchings and Wu (1987) found extensive deterioration of the coral reefs of Hainan Island, South China Sea, in 1984. Dustan and Halas (1987) found degradation of a Florida coral reef between 1975 and 1982-83 due to physical disturbances in the shallows and sediments and disease deeper. Porter and White (1988) found degradation of reefs in the Florida Keys at least in the shallows, but less degradation deeper, during a 1983-86 study. Jaap (1988) noted that human activities also affect reef development in Florida and that contamination of the reefs was caused by urbanization of the coastal fringe. Ogden (1989) noted a "precipitous decline in environmental health" of the Florida Keys' coral reefs. Trace metals, halogenated hydrocarbons, PCB's, plasticizing agents and coliform bacteria were found in the sediments and organisms from coral reefs in Florida (Skinner and Jaap, 1986; Glynn and Szmant in Jaap, 1988). Acevedo and Goenaga (1986) found that land clearing was causing rapid degeneration of coral reefs in Puerto Rico. Acevedo et al. (1989) found deterioration of reefs near Ponce, Puerto Rico due to sediment impact. Moore in Anonymous (1988) noted deterioration of the coral reefs in Barbados. Naim (PC) noted chronic nutrient enrichment in corals which bleached at Reunion Island in 1988. Deterioration of coral reefs, possibly, has had a synergistic effect on bleaching. These long-term damages may have also reduced the resilience or the level of resistance of coral reef hosts to disturbances such as bleaching events.

Exceptionally intense bleaching in presumably pristine areas such as the Dry Tortugas (Voss, 1989); San Salvador, Bahamas (Gerace PC, Hardy PC) and Mona Island seems to negate the possibility of human effects and deterioration on intensifying bleaching. Possibly deterioration of coral reefs is no longer localized near disturbances caused by humans. Increased nutrient input disrupts the hermatypic coral reef community (Hallock and Schlager, 1986). Wide-spread increase in nutrification that is detrimental to coral reefs has been suggested by Lapointe (1989) and Shinn (1989).

## TEMPERATURE

Brief water temperatures 3-4°C above the normal maximum, or extended periods 1-2°C above the maximum, will bleach corals (Jokiel and Coles, 1977). Yamazato (1981) suggested that bleaching in Okinawa in 1980 was caused by elevated seawater temperatures. The 1980 bleaching in Australia was shorter and less extensive than that in 1982 or 1983, but similar in species affected. Unfortunately, little detailed information was obtained in 1980 (Oliver, 1985), but the bleaching occurred in the warmwater period as did the 1980 bleaching events in other parts of the world, and all may be related. Bleaching in 1983 was closely correlated with sea warming in the tropical eastern Pacific, Okinawa, Java Sea, Florida Keys, and parts of the western Caribbean (Glynn, 1984a,b; 1988a). Carpenter in Hollings (1988) suggests that temperature caused bleaching in the western Caribbean. Increased temperatures seemed to be the most likely cause of bleaching at Reunion Island (Faure PC), Indonesia (Suharsono, 1988), Seribu Islands and Karimuh Java Islands, Java Sea (Soekarno PC) in 1983. Oliver (1985) and Harriott (1985) suggest that high water temperatures were involved in the 1982 bleaching of the Great Barrier Reef, but Fisk and Done (1985) reported normal summer temperatures before and during the 1982 bleaching in Australia. Glynn (1988a) and Glynn and D'Croz (1989) simulated the temperature conditions of the 1982-1983 ENSO event in the eastern Pacific and produced bleaching, death of corals and histological conditions identical to the original observations. Bleaching in the Galápagos Islands in 1987 occurred at the height of a 2-3°C positive sea surface temperature anomaly (Glynn et al., 1989). Most reports suggested higher than normal temperatures occurred during the 1987 bleaching (Williams, L. and Williams, 1987; Williams et al., 1987; Jaap in Hollings, 1988; Williams and Lang, 1988; Williams, E. and Williams, 1988a,b).

Elevated water temperature was suggested as the cause or as a probable cause of the 1987-88 event (D'Elia in Hollings, 1988; Jaap in Hollings, 1988; Lang, 1988c; Sandemann, 1988a,b; Wicklund in Hollings, 1988; Williams and Lang, 1988; Williams, E. and Williams, 1988a,b; Lang et al., 1989); and for local events in the Bahamas (Wicklund in Hollings, 1988), Colombia (Bohorquez, 1988), Florida Keys (Causey, 1988; Hudson, 1988; Jaap, 1988), Jamaica (Gates in Woodley, 1988; Sandeman, 1988b) and Tobago (Risk PC). Newton (PC) suggests *Agaricia lamarcki* is a cooler water coral found on the intermediate to deep portions of coral reefs. It was the most extensively bleached host in Bonaire in 1987. The pattern of bleaching, most severe in the more shallow portion of its depth range (above 35 m), suggests that temperature caused the observed bleaching (loc. cit.). He also noted above average water temperatures for the last quarter of 1987. Sponges, sea grasses, corals and sea urchins, *Diadema antillarum*, all died and/or bleached during a period of exceptionally high water temperatures in the Florida Keys in July and August 1983, and similar events occurred in 1987 (Causey PC, Table 23). Hyperthermia also killed non-zooxanthellate reef animals in the Gulf of California and Kenya during the 1987 bleaching, as previously discussed. These mortalities suggest that unusually high seawater temperatures occurred on some inshore areas during that time.

Hart and Scheibling (1988) suggested that a positive temperature anomaly in June 1960 caused the increase in populations of sea urchins which destroyed kelp beds in the U.S.A. in the 1960's and 1970's. Glynn (1988b) documents a variety of world-wide damage caused by the 1982-83 ENSO event. Although a variety of destructive ENSO effects were involved (as discussed previously), the most important detrimental effects to marine organisms was the seawater warming accompanying this event. Vicente (1989) documents the demise of a group of sponges from much of the Caribbean related to slight increases in seawater temperatures since early in this century. He also suggests that the epizootic ravaging commercial sponges in the Mediterranean since 1986 until the present (Table 23) may also be related to increases in sea surface temperatures in the Mediterranean Sea. The 1986-to-present time frame also coincides precisely with the present world-wide bleaching events. We do not know the timing of the mortalities of *Chondrilla nucula* in Puerto Rico (loc. cit.) and mangrove sponges in Belize (Ruetzler, 1988) in relation to the bleaching events.

Higher than normal water temperatures were also reported from many areas of the Indo-Pacific where bleaching occurred. Wood (1988) suggested that high water temperatures caused the bleaching in the Maldives. Water temperatures from May to July 1987 were estimated to be 2-3°C higher than normal, and the meterological office, Bracknell, England, considers the February-July sea surface temperatures from the vicinity of the Maldives (75°E, 5°N) to be abnormally high (Wood, 1988). Reyes-B. (1988) suggested the high (>30°C) temperatures in the Gulf of California probably caused coral bleaching, but does not dismiss the possibility of a synergistic effect of light. Beckman (PC) noted high temperatures during the January-February 1988 bleaching and mortalities in Fiji. Lucas (PC) noted bleaching of giant clams on the Great Barrier Reef due to high water temperatures. Goggin and Lester (1988) found that warmwater temperature stress of giant clams infected with parasites (*Perkinsus* sp.) can produce mortalities. Other species in this genus of parasite produce mass mortalities of mollusks during the warmwater periods in North America and Europe (Azeredo, 1989; Table 23). High water temperatures in September-October (27.5° C) were also blamed for the bleaching in the Hawaiian Islands in 1986 (Choquette PC) and 1987 (Choquette PC, Hau PC). Warmwater temperatures were noted during bleaching in Kenya (McClanahan PC).

No bleaching was recorded from Bermuda in 1987 although coral reefs were carefully monitored (Cook PC). In 1988, Bermuda experienced the warmest summer in 30 years (records of the Department of Agriculture, loc. cit.). Bleaching began with the water temperatures exceeding 29°C. As described previously, a bout of bleaching occurred world-wide during the warmwater period of 1988. Warm, very clear waters, occurred during this event in the Florida Keys (Causey PC), warm, very still waters in Jamaica (Gates PC), and warm and turbid waters in Colombia (Zea PC).

High light intensity caused substantial loss of zooxanthellae pigments in corals in long-term growth experiments (Coles and Jokiel, 1978). Hoegh-G. and Smith (1988a,b) suggest increased levels of light bleach hosts by removing pigments, while increased temperatures bleach by removing zooxanthellae. If this is true for the 1987-88 event, then temperature was the primary cause because those hosts examined possessed 10% (Gladfelter, 1988; Glynn, 1988a) or 10-20% (Reese et al., 1988) of the normal levels of zooxanthellae. However, some increased light effects may also be involved, as the remaining cells possessed reduced levels of pigments (Gladfelter, 1988; Glynn, 1988a).

Porter in Woodley (1988) observed bleaching in deep *Agaricia* spp. for a number of years on transects in Jamaica during the period of warmest water temperatures in October. In 1987, these "October" temperatures were attained several months early and remained several months later than usual (Gates in Woodley, 1988; Sandeman, 1988b). Since these temperatures are known to cause bleaching in a few corals over a short period of time, it is not surprising to find long-term maintanence of these levels to cause massive bleaching. Antonius (1988) also found bleaching in the eastern Red Sea for the last 6 years during the warmwater period of the year. Elevated temperature is one of the few reasonably constant trends that we can find in our highly variable reports. The most intense, extensive and destructive bleaching in 1980, 1983 and 1987-88 has either occurred along with unusually elevated seawater temperatures, or, when temperature data were not available, during the normal warmwater season. Even the 1979, 1982 and 1986 events fall into these warmwater periods. If the less severe mid- to late 1988 bleaching is considered a separate event, these disturbances would also fall largely into this period. This is somewhat obscured in Figure 3, because the warmwater seasons are at different times of the year in the southern and northern hemispheres. Fortunately, the times of highest seawater temperatures follow considerably after the times of most intense direct solar radiation to conviently separate the 2 effects. High water temperatures usually persist much longer than the periods of most direct solar radiation. In the rare case (Bermuda 1988) where both temperature and the onset of bleaching were carefully monitored, bleaching exactly coincided with an unusual increase in the seawater temperature (Cook PC). In the unusual case (eastern Pacific 1983) where exact seawater temperatures were available at numerous locations throughout an event, the bleaching was more intense where temperatures were higher (Glynn et al., 1989). Furthermore, a controlled experiment duplicating the conditions recorded in the eastern Pacific in 1983 has demonstrated that the coral reef bleaching, tissue damage, and mortalities can be caused by temperature alone (Glynn and D'Croz, 1989). While world-wide bleaching events are too complex to have a single, simple cause, temperature seems to be the most important, the unifying or triggering cause.

No unusually high temperatures were recorded in Panama (Knowlton, 1988), and the elevations of temperature at Lee Stocking Island, Bahamas (Lang, 1988a,c), parts of Colombia and the Flower Garden Banks, Texas, were slight (Lang PC). Bleaching was also slight in Panama and Texas and moderate in the beginning in Colombia. Atwood et al. (1988) noted increased sea surface temperatures (SST) occurred off Puerto Rico in 1981 similar to those seen in 1987, but bleaching did not occur in 1981. Actually, some bleaching did occur in Puerto Rico in 1981, but has only recently been noted (Williams et al., 1987). MacFarlane and Goreau (1988) suggested past temperature records show significantly higher temperatures have occurred in Jamaica without noticeable bleaching. The difference in effect can probably be explained by the unusual length of time for the 1987 elevations. While normal SST prevailed over much of the region of most intense bleaching (Atwood et al., 1988), abnormally high inshore temperatures occurred (where measured) in many areas. Since offshore SST's are known to have been lower than inshore temperatures in many locations, the use of offshore SST data in general to discredit inshore temperature as a cause for bleaching over the entire region (loc. cit.) was puzzling. Bleaching was highly correlated with elevated SST in the eastern Pacific in 1983 (Glynn, 1988a; Glynn et al., 1989). The overall seawater temperatures alone (represented by SST) may have not caused bleaching in 1987, as it did in the eastern Pacific and other areas in the 1983 event. In most areas in 1987, temperature increases which caused bleaching were due to weather conditions that allowed inshore heating and not ocean-wide, elevated seawater temperatures.

In 1987 a second bout of bleaching occurred in November-December (Table 15) when temperatures were falling, and a third bout occurred (February-March 1988) in some areas long after temperatures had dropped. The third bout was possibly a result of a sudden lowering of water temperatures in the Bahamas (Lang PC), upwelling of cooler waters in south Florida (Vose PC), and possibly cool temperatures in Puerto Rico. The March-April 1989 bout in the Gulf of California was caused by low water temperatures (Table 15)(Baynes PC), and those at Mona Island, Puerto Rico and the U. S. Virgin Islands were associated with the lowest temperature time of the year following an unusually cool spring. A cold current and possibly upwelling (10-14°C) in Taiwan in November 1988 bleached most faviids between 5 and 20 m along the east side of Nanwan Bay (Dai PC). The possibility that coral reef hosts may be more prone to bleaching by low temperature following a severe high temperature bleaching event is suggested by these cold "echo" bouts. These bouts only produced minor amounts of bleaching and do not detract from the assumption that elevated seawater temperatures accompany the most intensive and wide-spread bleaching of coral reef hosts.

If unusual water temperatures caused the world-wide coral reef bleaching events, then temperatures must have increased prior to 1979-80 when these events first occurred and must have increased again between 1979-80 and 1986-88 to cause even more severe events. Partial to short term, limited bleaching has been recorded in recent years (Smit-V. PC) in deep-water *Agaricia* sp. off Jamaica (Porter in Woodley, 1988), for the last 6 years in coral reef hosts in the Red Sea (Antonius, 1988), for 10 years in *Palythoa caribbea* off St. Croix (Gladfelter PC), and for the last 10-15 years in coral reef hosts off the Maldives (Wood, 1988). Chronic bleaching has occurred in Cuba over the last 10 years (Ibarra-M. PC). Whether these minor bleaching bouts were more severe in 1983, 86, and 87 would be of interest, but they are more important in establishing a pattern of bleaching during the last 6-10 years, mostly during warmwater periods. Vicente (1989) noted the continuing temperature increase in the last 50 years, which has eliminated some sponges from the Caribbean. A major predator (sea star) experienced catastrophic decline in the Gulf of California due to prolonged elevated temperatures (Dungan et al., 1982)(Table 23). Lopez (PC) noted mortalities of herrings (*Harengula* spp.) possibly caused by high temperatures in Puerto Rico in the last few years and Vicente (PC) noted less extensive bleaching in Puerto Rico in the warmwater period of 1981. Wood (1988) noted slightly higher temperatures for the last 10 years in the Indian Ocean (Meterological Office, Bracknell, England). Cook (PC) and Katz and Hagen (1989) found the summer of 1988 was the warmest in Bermuda for 30 years. Sea surface temperatures in Puerto Rico have been on an upward trend for the past few years (Corredor PC). Southern ocean temperatures in 1987 were the warmest for the past 100 years (National Climate Program Annual Report 1987, 1988). Buddemeier and Smith (1988) suspected but could not prove that greenhouse effect rises in global temperature have already begun. The 4 warmest years of the last 100 (since temperatures have been recorded by instruments) were all in the 1980's and 1987 was the warmest (Kerr, 1988). Global temperature has increased approximately 0.5°C since 1880. The warming surge since 1965 is raising the temperature of the earth to levels that rival the warmest temperatures since the last ice age (loc. cit.). The decade of the 1980's was significantly warmer than any previous period on record (National Climate Program Annual Report 1987, 1988). Coral reefs may be the first conspicuous casualty of global warming, and certainly indicate how drastic the effects of the predicted warming may be.

## MISCELLANEOUS

A number of other potential factors favoring bleaching were reported, but these varied with almost each location. Greater bleaching was reported in areas of increased sedimentation in Puerto Rico (Morelock PC); and more sediments and suspended matter were noted during the event in the Florida Keys (Hunt PC, Bohnsack PC); Bahamas (Bland PC); Mayotte Reef west Indian Ocean (Faure PC). Murky, silted, freshwater runoff was reported in Colombia (Lang, 1987; Sanchez-R. and Gomez-R., 1987; Duque-T. and Zea PC; Solano PC), Venezuela (Losada, 1988), and in Culebra Island (Perkins PC). Siltation damaged reefs in the Andaman Islands (Indian Ocean) which also suffered bleaching (Wood PC). Cyclone "Clorilda" preceded the event in Mayotte Island (Faure PC) and freak high tides and waves caused siginificant damage to coral reefs in the Maldives (Wood, 1988). Abnormal sea level, sea state, disturbances associated with the 1982-83 ENSO event were summarized by Glynn (1988b). Long-term sediment stress and contamination of coral reefs by urban areas was noted in Florida (Jaap, 1988); and pesticides in coral tissues in Panama (Glynn, 1984a; Glynn et al., 1984). All Caribbean reefs are affected by pollution (Wicklund in Hollings, 1988). Some reefs in Puerto Rico adjacent to urban areas may have bleached more intensly than more isolated areas. A combination of stresses may have been necessary to start the bleaching in some areas (Lang, 1988a,c) and reefs subjected to sediment or pollution seemed to have bleached more intensely (Williams and Lang, 1988). Multiple factors may act synergistically and produce greater bleaching than individual stresses would alone (Coles and Jokiel, 1978; Steen and Muscatine, 1987). Natural coral reef bleaching is usually caused by synergistic effect among several factors (Lang in Hollings, 1988).

## COMPOUNDING DISTURBANCES

A large number of major marine ecological disturbances have occurred in the last few years (Table 23). Some of these have had a direct impact on the damage caused by coral reef bleaching and/or the recovery of bleached hosts:

(1) **BLACK LONGSPINED SEA URCHIN MASS MORTALITY:** Many algae grow more rapidly than corals and would overgrow and smother coral reefs if not controlled by herbivorous urchins and fishes (Little and Littler, 1985). The 1983-84 *Diadema antillarum* mass mortality effectively eliminated one of the potentially most important controllers of algae on western Atlantic coral reefs. This is especially serious where overfishing has already removed many herbivorous fishes (Hay and Taylor, 1985). Rogers (1985) found all shallow water coral reef fisheries in the Western Atlantic had declined due to overfishing and habitat destruction. Lang in Hollings (1988) suggests that almost all commercial fisheries in the tropical western Atlantic are overfished and are highly vulnerable to disruption. Unchecked algal growth is occurring at the expense of reef corals in many central Caribbean areas where this double loss of algae controlling herbivores has occurred (Lang in Hollings, 1988). Carpenter in Hollings (1988) suggested that the great increase in algae on Caribbean coral reefs which in some cases has overgrown and killed corals was an effect of the *D. antillarum* loss. After the *D. antillarum* mortality, algal blooms occurred on many reefs in the Caribbean, recruitment rates of corals became reduced and a reduction of coral cover followed. Some adult corals, gorgonians, zooanthids and sponges were overgrown and killed by algae (as summarized by Lessios, 1988). Acevedo and Morelock (1988), monitoring sediment stressed corals off Puerto Rico, noted colonization by filamentous algae. Many of our reports of the coral reef bleaching in the Caribbean noted rapid growth of algae on bleached and dying corals. Vicente (1989) reports the recent decline of populations of a sponge (*Chondrilla nucula*) due to overgrowth by filamentous algae. Causey (PC) noted large amounts of blue-green algae covering sand areas between corals in the Florida Keys which did not occur prior to the *D. antillarum* loss and Zann (PC) noted large-scale benthic algal blooms on the Great Barrier Reef prior to and during the 1987 event. In the Indo-Pacific, with no diadematid loss (except in the Hawaiian Islands) fewer cases of algal damage have been noted. Cuet et al. (1988) found fleshy algae overwhelming corals on Reunion Island, Indian Ocean. Algal growth was damaging corals in some areas there prior to the 1987-88 coral reef bleaching (loc. cit.). Algae were more abundant on Atlantic reefs after the *D. antillarum* mortality, and may have been more available to take advantage of injured or dying corals, and may have contributed to the damage and mortalities which occurred during the event. Bare skeletal surfaces on colonies were quickly overgrown by algae. The former high abundance of *D. antillarum* might have kept some of the surfaces clear of algae and available for eventual recovery by the colony. All dead areas of colonies (which were followed by those making reports) were quickly overgrown by algae. Another urchin, *Tripneustes ventricosus*, has been drastically reduced in numbers, presumably by overfishing, in Barbados during the 1980's (Scheibling and Mladenov, 1987). Overfishing for herbivorous fishes and urchins will certainly intensify the algae problem on the reefs. Goenaga et al. (1989) noted that *Montastrea annularis* colonies quickly recovered from physical damage prior to the 1987 bleaching, but most areas damaged during and after this event permanently lost tissue.

(2) **WHITE BAND DISEASE EPIZOOTICS:** In the late 1970's large stands of *Acropora palmata* began to die of WBD. This mortality continued until the majority of this coral in the region was destroyed (Carpenter in Hollings, 1988); loss of *A. cervicornis* has also been considerable. In the

summer of 1980, epizootics of WBD occurred in Curaçao (*Acropora* spp. 70-90% affected) and Jamaica (Rogers, 1985) Between 1981 and 1986 *A. cervicornis* declined 96% at Key Largo, Florida Keys (Jaap et al., 1988). Most colonies of *A. cervicornis*, which was formerly a dominant coral on the reef slopes at about 5 m, Islas del Rosario, Colombia, died during the early 1980's (Lang, 1988a,c). *Acropora* spp. died in Costa Rica and possibly Colombia after the 1983 bleaching event (loc. cit.). *Acropora cervicornis* was reduced 99% a few years ago in Curacao by WBD. Storm damage has hindered the slow recovery of this coral, and recovery may not be complete for another 20 years (van Duyl, 1989). Large areas of *A. cervicornis* died in San Salvador, Bahamas, in the fall of 1986 (at approximately the time bleaching was occurring elsewhere). A mass mortality of *A. cervicornis* occurred off Panama (Knowlton et al., 1988). Mortalities of *A. cervicornis* in the beginning of the 1987-88 event in Jamaica (Woodley PC) and the Florida Keys (Jaap in Hollings, 1988) may have been related to WBD. Mortalities of *A. cervicornis* in the Bahamas (Lang in Hollings, 1988) and *A. palmata* in the Florida Keys (Lang PC) may have been compounded by WBD. Bohorquez (1988) found WBD in some of the corals bleached in Colombia. Some of the bleaching of *Acropora* spp. in the Andaman Islands, Indian Ocean, in February 1987 may have been caused or compounded by WBD. Both WBD and BBD have been noted on these reefs (Wood PC). The combination of WBD and bleaching must be more lethal than either disturbance alone. Fortunately the ongoing study of WBD under the support of Sea Grant (Hernandez-A. PC) and the monitoring of this disease by the Virgin Islands Resource Management Cooperative (Davis et al., 1986) in the U. S. Virgin Islands should provide more information about this combination.

(3) BLACK BAND DISEASE OUTBREAKS: An outbreak of BBD occurred in the Florida Keys from August through September 1987 during the coral reef bleaching event (Causey PC). Dill in Hollings (1988) noted BBD in bleached corals during the event in the Bahamas, and suggested that the disease was expanding in the area. Lott (PC) found BBD only in bleached *Siderastrea* spp. during the event in the Turks and Caicos; Bohorquez (1988) found some BBD in bleached corals in Colombia and Wood (PC) noted BBD from reefs in the Andaman Islands (Indian Ocean) where bleaching damage occurred. BBD occurred in *Diplora clivosa* on Mona island in March 1989. All colonies (300+) of *Siderastrea siderea* and *S. radians* we examined from 4 locations on Mona Island 9-10 March 1989 were either partially bleached and/or diseased, but only a few showed positive signs of BBD. We also noted BBD at 2 sites off southwestern Puerto Rico in *Montastrea annularis* and possibly *S. siderea*. This disease had not been noted at Mona Island or Puerto Rico in previous extensive studies (Goenaga PC). Colonies infected with BBD may be less resistent to bleaching. The outbreaks of BBD in Florida and possibly Mona Island and its spread in the Bahamas during the 1987-88 bleaching event indicate some advantage for this disease in corals damaged by bleaching, possibly a breakdown of resistance. Shinn (1989) found that many corals weakened by bleaching in 1987 subsequently died of diseases.

(4) OTHER DISEASES OF HOSTS: Besides WBD and BBD, a number of other disease conditions have been reported from bleached hosts or from hosts during the time of bleaching. Some of these appear, with the limited information available, to describe degenerative conditions, caused or intensified by bleaching, or possibly by the conditions which caused bleaching. Shinn (1989) suggested that coral diseases were related to the world-wide rise in sea level and an overabundance of nutrients. Gladfelter (1988) suggested that bleached corals may be susceptable to other stresses and D'Elia in Hollings (1988) suggests that they are more susceptable to diseases which can kill corals. A normal skelatal fungus of *Millepora complanata* invaded and decomposed the tissues of this coral during bleaching in 1983 (Jaap in Hollings, 1988; Te Strake et al., 1988) and in 1987 (Jaap, 1988). Vicente (1989) recently found *Chondrilla nucula* succumbing to overgrowth by filamentous algae in Puerto Rico. This sponge also bleached in Puerto Rico during the 1987-88 event (Williams and Bunkley-W., 1989). Ruetzler (1988) describes mortalities of a mangrove sponge caused by its symbiotic cyanobacteria. Unexplained sponge mortalities occurred in Puerto Rico (Williams and Bunkley-W., 1989) and in the Florida Keys (Causey PC) in 1987.

(5) CROWN OF THORNS OUTBREAKS: *Acanthaster planci* damage has probably compounded the coral reef bleaching event by outbreaks which preceeded the 1987-88 disturbance in many areas, and by preying on survivors in others. A new series of *A. planci* infestations began in many areas of the Great Barrier Reef of Australia (and possibly elsewhere in the Pacific) in the late 1970's and

is continuing (Phillips, 1987). Outbreaks of *A. planci* have occurred in the past at intervals of several decades (2-3 times a century), but they are much more frequent now and are chronic in some areas (Birkeland, 1989; Yamaguchi, 1986). Infestations in 1981-83 also preceeded the 1983 bleaching in Mayotte Island (Thomassin PC) and occurred along with bleaching damage in the Andaman Islands (Indian Ocean) (Wood PC). Muzik (1985) found coral reefs of the Ryukyu Archipeligo, Japan, had not recovered from *A. palanci* damage 10 years previously and were largely dead. She (PC) suggests that bleaching was not noted in many areas because too few hosts remain alive to register bleaching. *A. planci* damage to coral reefs may have weakened or predisposed corals to bleaching. Bleaching also increased the vulnerability of some surviving corals, formerly protected by barriers of *A. planci*-resistant corals, when these corals perished in the bleaching event in Panama in 1983 (Glynn, 1985b) and the Maldives in 1987 (Wood, 1988). Corals died during or after the bleaching in many areas, but few reports noted non-photosymbiotic animal damage in 1987-88. Presumably, the ratio of *A. planci* to prey corals may have increased in many areas as a result of the bleaching. Even when non-photosymbiotic animals were damaged, as in the eastern Pacific during the 1982-83 bleaching event, the relative effect of *A. planci* predation intensified (Glynn, 1985b).

(6) **OTHER CORALLIVORE/BIOERODER OUTBREAKS:** McClanahan and Muthiga (1988) found overfishing on Kenyan coral reefs greatly increased the numbers of the sea urchin, *Echinometra mathaei*, and decreased coral cover. Intense bleaching and host mass mortalities occurred on Kenyan coral reefs in 1987 (McClanahan PC). Whether more intense bleaching occurred on the reefs most damaged by overfishing and urchins was not determined. Sea urchins on some eastern Pacific reefs from early 1983 to at least late 1987 were destroying the reef framework (Glynn, 1988b). Corallivorous gastropods, *Drupella* spp., are causing extensive damage to corals in Miyake-jima, Japan, the Philipines, and Ningaloo Marine Park (western Australia), and dense aggregations occur in much smaller areas at Guam and Enewetak (Birkeland and Eldridge, 1988). Both *Drupella* spp. and *Echinometra mathaei* are extraordinarily abundant around Okinawa (loc. cit.). Of these areas, we have reports of bleaching in 1987-88 only from Okinawa. Knowlton et al. (1988) noted predators at near-normal levels prevented recovery of *Acropora cervicornis* following storm damage in Jamaica and following a mass mortality of this host in Panama. Glynn (1985a,b) and Guzman and Robertson (1988) noted damage by predators to bleaching corals in 1982-83, although the abundance of these predators was no higher than before the bleaching event. A combination of predator/bioeroder outbreaks and bleaching could be extremely serious. Glynn (1988b) found damselfishes established territories in algal patches in necrotic areas caused by bleaching and caused further coral mortalities. We observed a tagged, bleached colony during the 1987 event with a small damselfish garden on its side. This stony coral colony became almost totally engulfed by the garden and died.

(7) **RED TIDES:** Red tide or dinoflagellate blooms commonly produce mass mortalities of marine animals following El Niño events, but none was reported after the 1982-83 event (Glynn, 1988b) and we only received one report for the 1987-88 event. From March-April of 1987 a toxic dinoflagellate bloom possibly occurred in the Maldives. Reports of "red water" were received from several locations and red scum washed ashore at Lakantinolla. Dead fish (mostly moray eels, trumpetfish, and anemonefishes) were found and many reef fishes were observed to behave in a disoriented manner at this time. Anemones on the reef closed (Wood, 1988). Unfortunately, samples of the apparent dinoflagellate bloom were not preserved. Red tides may have compounded the 1987-88 bleaching event in the Maldives. Red tides have been increasing in frequency of occurrence in the western Pacific since 1975 (Birkeland, 1989; Maclean, 1984).

## CONCLUSIONS

### WORLD-WIDE BLEACHING EVENTS

The 1987-88 bleaching was the most extensive and widespread ever recorded. It undoubtedly represents a world-wide interrelated disturbance (Fig. 2) as all cases can be arranged in an overlapping time-related representation (Fig. 3). The 1982-83 bleaching events (Glynn, 1984a,b) were less obviously related (Glynn, 1984b, 1988b). The most confusing part of the 1982-83 pattern was the extensive bleaching on the Great Barrier Reef of Australia in 1982, 1 year before the 1983 reports of bleaching. If the 1982 Australian event is temporarily ignored in our analysis, then the remaining disturbances (loc. cit.) seem to represent an interrelated world-wide event. Bleaching also occurred on the Great Barrier Reef in 1983, although it was not as intensive, it was almost as widespread as the 1982 event there (Oliver, 1985).

At least 3 widely separated areas in the Pacific suffered extensive coral reef bleaching in 1980: Australia (Oliver, 1985), Easter Island (Cea-E. and DiSalvo, 1982), and Okinawa (Yamazato, 1981). Mass zooxanthellae loss caused by high seawater temperatures also occurred at Enewetak in August 1979 (Fankboner and Reid, 1981). They (loc. cit.) assumed, without much information, that the expulsion was a routine summertime occurrence and not part of a bleaching event. These incidences were studied and reported separately and no effort was made to discover bleaching in other areas at that time. Bleaching also occurred in Florida in 1980, and a year earlier, extensive bleaching occurred in Bonaire. The wide distribution of the known 1979-80 bleaching sites (see arrows Fig. 2) almost covers as much of the world as the 1983 and 1987-88 bleaching sites, they only differ in the total number of sites. We suspect the 1979-80 events represent a first, possibly less intense and extensive (and/or possibly less well studied), world-wide interrelated bleaching disturbance. What has been recorded may represent only a fraction of the actual bleaching areas in 1979-80. No one expected or tried to confirm world-wide bleaching in 1980. The great distances between the locations of reported bleaching in 1979-80 also suggests that unreported events could have occurred in these areas. After 9 years, enough additional reports to confirm the world-wide nature of the disturbances in 1979-80 may never be obtained.

How else can the events in 1980 be compared with those of 1983 and 1987? Three years separate the first (1980) and second (1983) major events and 4 years occur between the second and third (1987). Each major bleaching event increased in extent and intensity. All 3 disturbances share another similarity, all were preceded by 1 year by extensive bleaching events at 1 or more locations. The 1979 bleaching in Bonaire preceded the 1980 bleaching disturbances by 1 year, the 1982 bleaching in Australia preceeded the 1983 bleachings by a year, and the bleaching at many sites in 1986 preceded the 1987-88 event by 1 year. This brings the 1982 bleaching in Australia, which we deferred comment on before, back into consideration, and explains how it fits into the pattern of world-wide bleaching. Even these "preceding bleaching events" intensified and enlarged. Therefore, the bleaching that occurred in 1979-80, 1982-83, and 1986-88 each formed a bleaching complex that included a preceding event followed by a main event.

### CAUSE OF THE 1986-88 EVENTS

The conflicting and contradictory causes reported and suggested among and even within sites makes analysis of the 1986-88 bleaching complex very difficult. The overall elevated temperatures for the 1980's made temperature effects an appealing suggestion for the cause of bleaching. The historic information, both published and new, related all extensive and severe bleaching, and even most minor bleaching, to the times of the year with the highest seawater temperatures, or other times with abnormal temperatures as high as these warmwater periods. The SST data (Atwood et al., 1988) conflicted with a direct temperature explanation, but inshore temperatures at the same time were high enough to cause bleaching, suggesting that poor circulation associated with world-wide ENSO effects was resulting in temperature increases of already very warm inshore waters to levels above that required for bleaching. These 2 ENSO warming effects (direct ENSO warming; and indirect warming inshore due to meterological effects associated with ENSO) explain the most intense and wide-spread of the 1986-88 bleaching bouts, and even explain most of the less intense bouts. Other

ENSO effects which caused bleaching directly, were important at only a few of the reported sites. Other ENSO effects, degradation effects, and light effects may have synergistically intensified bleaching.

## CAUSE OF THE 1982-83 EVENTS

Some of the 1982-83 bleaching bouts were probably caused by obvious increases in overall seawater temperature as indicated by the SST data (Glynn, 1984a; Glynn et al., 1989). Much of the remainder was probably due to ENSO effects which allowed local, inshore temperature to increase as in 1986-88. Since many local temperatures were not recorded or recorded for only brief periods, the role of temperature cannot be determined for many areas. The 20 temperature recorders in place in the Caribbean in 1988 (Wicklund PC) may help to obtain this information for future events just as a recorder in place on the coral reef in Okinawa confirmed temperature as the cause of the 1980 coral reef bleaching there (Yamazato, 1981). The underlying cause was again probably the increase in temperatures world-wide and the deterioration of coastal areas and coral reefs all over the world.

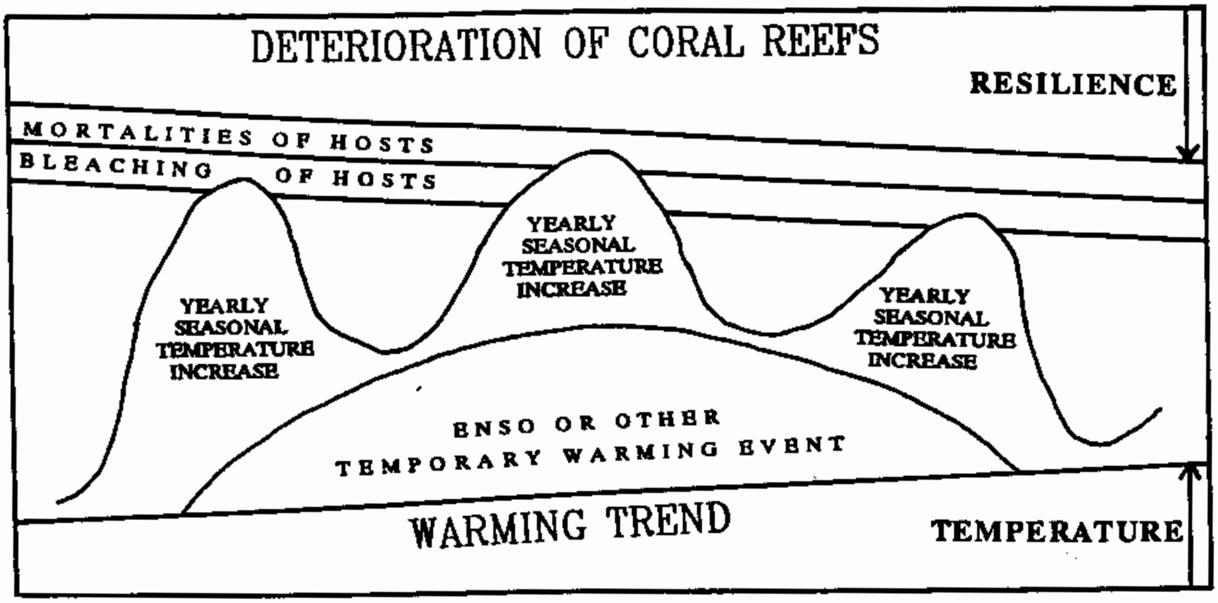

Figure 4: Model of the causes of world-wide coral reef bleaching. Elevated temperatures sufficient to bleach hosts are attained seasonally when augmented by the general warming trend and ENSO or other temporary warming events. The general deterioration of the coral reefs has lowered the resilience of the hosts making bleaching damage more serious. The three seasonal peaks of temperature also represent the preceding, main, and following events as shown in Figure 1. The preceding and following events only cause bleaching because they are on the "shoulders" of the temporary warming event; while the main event produces more severe bleaching and mortalities because it occurs at the height of the temporary warming event.

## THE 1991 OR 1992 CORAL REEF BLEACHING EVENTS

Our analysis of bleaching in the last decade, shows that three bleaching complexes have occurred suggesting a cyclic phenomenon (Fig. 1), probably riding on a progressively higher base of elevated temperature and increasing reef deterioration. If our model (Fig. 4) is correct, bleaching cycles will continue to occur on average every 3 to 4 years, with another bleaching complex predicted to begin with a preceding event in 1990 or 1991 and becoming a major world-wide bleaching event in 1991 or 1992. By our model, we expect the event to be more severe and more extensive than the others.

Since bleaching complexes also depend on the next moderate or strong ENSO event and these occurrences cannot be predicted (Glynn, 1988b), the start of the next bleaching complex cannot be exactly pinpointed.

## PRECEDING AND FOLLOWING EVENTS

The 1979-80, 1982-83, and 1986-88 coral reef bleaching complexes were divided into "preceding" and "main" events; in addition, in the 1986-88 complex a "following" event was also observed. Each of these events center around the warmwater period of each year. Even during an ENSO warming event, temperatures in most areas are highest during the normal warmweather periods. A general background warming over 2 years (1979-80 or 1982-83) includes 2 warmwater periods; over 3 years (1986-88), 3 warmwater periods. The reason preceding and following events are less intense and less destructive than main events is that they occur in the beginning or ending of the warming trend, when warming is less intense; while the main events occur at the height of the background warming effect (Fig. 4).

Part of the problem in studying major marine ecological disturbances (MMEDs) is the lack of warning and the speed of these events. This makes research efforts difficult to plan and standard research funding almost impossible to obtain on such short notice. In 1979, a potential year-in-advance warning of major coral reef bleaching (1980) first occurred. In 1982, this same warning was repeated but no one was recording, much less analyzing, these events. This warning devise should have been recognized and used at least by 1986 when it was repeated for the third time. The coral reef scientific community should have had a year (1986-87) to prepare for the study of the most extensive world-wide bleaching event ever recorded (1987-88). How much knowledge have we lost because of failure to keep and understand the most rudimentary records of MMEDs? We can envision no better argument for an "Alert and Communication Center" (which will be discussed later).

## CARIBBEAN BLEACHING PATTERNS IN 1987

Once we accept increases in temperature as the probable cause of world-wide coral reef bleaching, then much of the variation can be explained. Reefs with large platforms, surrounded by shallows, or obstructed by physical structures which intensify poor circulation (Florida, the Bahamas, the Greater Antilles) bleached first and most intensely in 1987. These areas may have also experienced calmer conditions than the remainder of the western Atlantic during the period of most intense bleaching. Those with darkened waters to absorb solar heat (Islas del Rosario, Colombia; Florida Keys) or those prone to hypersaline formations (Bahamas, Florida Keys, Culebra, PR) bleached with particular intensity. Those with good circulation, narrow shelves, open ocean (Lesser Antilles, Curaçao, Bonaire, Bermuda) or those which did not experience calm conditions (Panama, Venezuela, Tobago, Trinidad and Tobago) took much longer to bleach, and experienced less bleaching. Bermuda did not experience any unusually high temperatures in 1987 and did not bleach. In 1988, high seawater temperatures accompanied coral reef bleaching there. The many reports of particular sides of islands or sides of reefs bleaching more intensely may be more easily understood if the efficiency of circulation is a factor.

## WHY WORSE IN 1987 THAN 1983?

More extensive bleaching occurred in 1987 in the Caribbean and many parts of the Indo-Pacific during a modest ENSO event and fewer recorded SST anomalies, than in 1983 with a very severe ENSO event and more temperature anomalies. Overall, more bleaching occurred in more areas in 1987 than in 1983. We believe the 1987-88 event meterologically favored inshore temperature increases in more areas, also 1987 was a warmer year on average world-wide than 1983 (Kerr, 1988), deterioration of coral reefs was more advanced in 1987 and the resilience of coral reef hosts was less.

## EASTERN PACIFIC 1983 AND 1987 COMPARISON

The eastern Pacific bleached less in 1987 than in 1983, while in most areas bleaching was more intense in 1987 than 1983. Possibly, the more sensitive hosts had already been killed in the eastern Pacific in 1983 and were not available to register bleaching in 1987. A better explanation may be that reefs in the eastern Pacific are in areas that are less subject to inshore heating during calm conditions of the 1987 ENSO, or did not experience the calm conditions reported elsewhere. In contrast, the Florida Keys where bleaching is frequently correlated with ENSO events may be especially prone to indirect ENSO heating. The 1983 bleaching in the eastern Paific was through direct, overall seawater temperature increases, not just heating of inshore waters as in 1987. Quinn et al. (1987) classifies ENSO events to various strengths including "moderate", "strong", and "very strong". The bleaching related to direct heating may be associated only with very strong ENSO events, while the bleaching associated with calm conditions (indirect heating) may be associated with very strong to moderate ENSO events. Both types are devastating only because of the overall elevated background temperatures of the 1980's.

## INDO-PACIFIC BLEACHING

The Indo-Pacific has many more coral reefs than the western Atlantic, but has a much lower density of coral reef scientists. Consequently, fewer reports were received from this region (Fig. 1). The low response might indicate few cases or less intense bleaching in these areas. However, the bleaching on the Great Barrier Reef was the most extensive and intense ever reported (Oliver PC, Zann PC) and the bleaching in the Maldives was intensive and extensive (Wood, 1988). Furthermore, the distribution of cases generally covers the entire region. We suspect that Indo-Pacific bleaching has been underreported. Other factors may have complicated the recognition of bleaching. In the eastern Pacific whole reefs were destroyed in 1983, and some coral species suffered extirpation (Glynn, 1984a; Glynn et al., 1989). Additional corals perished there in 1985 (Guzman et al., 1988) and the damaged reefs further eroded (Glynn, 1987) and suffered intense predation (Glynn, 1985a,b). There may be few hosts to bleach in some areas of the eastern Pacific. During the 1986-88 bleaching, new outbreaks of *Acanthaster planci* occurred on many Indo-Pacific reefs (Phillips, 1987). Their damage resembles bleaching and some bleaching may have gone unreported because it was attributed to *A. planci*.

## FUTURE CORAL REEF BLEACHING

Limited histological examination suggests that photosymbiotic hosts cannot recover completely from bleaching in 2 years (Glynn and DeCroz, 1989). Since the period between main events has been 3-4 years and 2-3 years separate complexes, repeatedly bleached hosts would presumably fare worse with each bleaching bout. In past events, bleaching was sporatic and all geographic areas were not affected in each event. If future cycles become more widespread, there may not be sufficient time for complete recovery between local bleaching bouts and bleaching may become more devastating even with no increase in severity. This may have already happened in some areas (such as the Florida Keys) where bleaching occurred during all world-wide complexes. Examples of this problem can also be seen in the Gulf of California (Table 15) and Jamaica (Goreau PC) where more severe bleaching occurred 2 years after the 1987 event. Certainly these areas had not recovered from the intense 1987 bleaching.

If we are correct about temperature increases, the deterioration of the coral reefs, and ENSO events driving coral reef bleaching; then the upward spiral of bleaching damage in this cyclic process can only increase. All predictions indicate continued increases in temperature. All recent evaluations of coral reefs have found continuing and accelerating deterioration. We can find no evidence that either situation will stabilize or improve. Some variation is expected, but deterioration and temperture rises will continue and ENSO events are unlikely to cease. Coral reef bleaching complexes will probably increase in extent and severity.

If we have correctly identified the causes of bleaching, we can forsee this process causing increasing devastation to photosymbiotic hosts. Ultimately, we expect these hosts will no longer form a significant component of the former coral reef community and these systems will be profoundly different.

## CONSEQUENCES

Cea-E. and DiSalvo (1982) and Gladfelter (1988) suggest that growth and carbonate productivity of bleached corals may be seriously reduced. Reese et al. (1988) found that while non-bleached corals grew 2 mm of new skeleton, growth was not detectable in bleached and partially bleached colonies. The consequences of coral reef bleaching range from loss of energy of reef hosts for a few weeks to total replacement of the benthic community (Jaap, 1988). Following the 1983 event in the eastern Pacific, species suffered extirpation, whole reefs died, and bioeroders threaten to destroy the remaining reef structures (Glynn, 1987). Knowlton (1988) noted that Atlantic reefs are dominated by hosts whose life histories make rapid recovery from catastrophic mortalities very unlikely. Two of the most important, most rapidly growing reef-building corals in the Atlantic recently have been seriously reduced in abundance by WBD (Table 23). Buddemeier and Smith (1988) recently predicted the demise of coral reefs by rapidly rising sea level. Graus and Mcintyre (1988) used a computer model to show that no Caribbean reefs will keep pace with the predicted sea level rise, higher waves will resuspend previously deposited sediment, and some entire reefs may die. They assumed that growth of *Acropora palmata* and *A. cervicornis* may keep pace with sealevel rise in the beginning, but they did not consider the WBD damage these corals are suffering. The increases in temperature associated with the "greenhouse effect" may destroy the reefs before they can drown. If temperature increases are causing the world-wide coral reef bleaching events, it may be a preview of what problems even small increases can cause (Wicklund in Hollings, 1988). Loss of much of the coral reefs may futher accelerate the "greenhouse" process. Coral reefs form an important buffer in the global carbon dioxide cycle (Lang in Hollings, 1988; Buddemeier, 1989), as calcium carbonate is one of the most important reservoirs of atmospheric carbon dioxide (Ohde, 1988).

All of the changes in the environment of coral reefs appear to be impacts caused by humans. Sedimentation, nutrification and pollution through direct human actions; increased seawater temperatures and sealevel rising, and possible UV light, through atmospheric additions. Other major marine ecological disturbances (Table 23) may also be related to these human impacts. Modification of human activities to cease or moderate these processes is probably physically possible, but the probability of this happening is low because the political and economic costs are so great.

Grigg (1989) suggests that coral reefs are "robust" ecosystems which have overcome the effects of rapid sealevel rise and other negative effects in the past and will do so in the future. It has been suggested (Jackson and Hughes, 1985) that drastic damage to coral reefs in the past has led to increased diversity of species on the reefs and aided in the success of the system. In those times, impacts were simple and direct, while the present ones are multiple and complex. Past damage occurred in a healthy system, while the present system seems already to be showing signs of deterioration.

If global temperatures continue gradually increasing, then extensive coral reef bleaching will eventually occur during every warmwater period in much of the tropics without aid of ENSO warming events. Whether most coral reef hosts in these areas survive until overall SST increases to that point depends on the severity and frequency of ENSO warming. The temperature increases should make portions of the former temperate zones more temperature-suitable for hosts as portions of the tropics become too hot for them. Unfortunately, the temperate zones are too high in nutrients to be suitable for most hosts (which require nutrient poor waters). These increases will also be accompanied by coastal flooding (Buddemeier and Smith, 1988) which will produce nutrient levels and sedimentation in almost all coastal areas detrimental to host growth and survival (Hallock and Schlager, 1986). ENSO warming may be providing a preview of the effects that increasing temperatures and increasing deterioration will have on coral reefs. The fragile coral reefs, in turn, may be providing a preview of more widespread disturbances.

## RELATED MAJOR MARINE ECOLOGICAL DISTURBANCES

Major marine ecological disturbances have recently increased in number and severity both regionally (Phillips, 1987; Williams, E. and Williams, 1987; Birkeland, 1989; Table 23) and globally (Birkland and Eldredge, 1988; Sindermann, 1988; Williams and Bunkley-W., 1988, 1989; White, 1989; Table 23). Some of the increase in number of reports could be due to increased number of observers (Birkland and Eldredge, 1988) or an increased awareness of the problem, but most of these disturbances are too obvious to have been previously ignored. Disturbances are spreading to new geographic areas (Bonaventura and Bonaventura, 1988; Tester, 1988; White, 1988, 1989) and wholely new or unknown diseases are erupting (Anonymous, 1989; Bird and Wright, 1989). Many of these disturbances share the quasi-synchronous timing, complexity, and high variation of the coral reef bleaching events (Phillips, 1987; Williams, E. and Williams, 1987; Sindermann, 1988; Williams and

Table 23: Other Recent Major Marine Ecological Disturbances.[1]

| DATE | ORGANISM AFFECTED | LOCALITY | SOURCE |
|---|---|---|---|
| Since mid-1800's | Mass fish kills (red tide) (*Ptychodiscus brevis*) | Gulf of Mexico | White 1988 |
| Since 1900, but more common in recent years(?) | Crustacean shell disease syndrome | World-wide high incidence in crowded or degraded habitats | Sindermann 1989 |
| Since mid-1960's | Mass kills of fishes (*Gyrodinium aureolum*)(red tide) | Europe | White 1988 |
| 1965 | Mass shellfish and fish kills (*Gyrodinium aureolum*)(red tide) | Omura Bay, Japan | White 1988 |
| 1966, 1976, 1981, 1982 | Caged and wild fishes and invertebrates (red tide) (*Gyrodinium aureolum*) | Norwegian Coast | White 1988 |
| 1969 - present | Chronic outbreaks (*Acanthaster planci*) | Ryukyu Islands | Yamaguchi 1986<br>Birkeland 1989 |
| 1969 - present | Red tides spreading and increasing in frequency | World-wide | White 1989 |
| 1970 - 1985 | Cultured yellowtail mortalities (*Chattonella antiqua*)(red tide) | Japan | White 1988 |
| July 1973 | Mass kill of cultured fishes (*Heterosigma akashino*)(red tide) | Ireland | White 1988 |
| Mostly mid- to late 1970's to present | Ulcerative diseases in coastal/esturine fishes | World-wide | Sinderman 1988 |
| 1975 - present | Red tides, dinoflagellate blooms and paralytic shellfish poisoning increasing at a geometric rate | western Pacific | Birkeland 1989<br>Holmes and Catherine 1985<br>McClean 1984 |
| 1976, 1979 | Mass mortality of Atlantic herring (*Gonyaulax excavata*)(red tide) | Bay of Fundy, Canada | White 1988 |
| 1977 | Outbreak and severe damage by *Acanthaster planci* | American Samoa | Kluge-E. PC |
| 1977 - present | Coral mass mortality (*Acropora cervicornis*) | Greater Caribbean Region | Carpenter in Hollings 1988 |
| 1978 | Mass mortality of sand lance (paralytic shellfish toxins) | Cape Cod, Massachusetts | White 1988 |

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|---|---|---|---|
| Summer 1978 | Sea star mass mortality (*Heliaster kubiniji*, *Othilia tenuispina*) | Gulf of California | Dugan et al. 1982 |
| August 1978 | Sponge mass mortality (*Xestospongia muta*) | Florida Keys, USA | Causey PC |
| Summer 1978<br>Summer 1979 | Mass mortality of sea stars, sea cucumbers (*Piaster* spp., *Patiria miniata*, *Stichopus parvimensis*) | southern California | Dugan et al. 1982 |
| 1978 - present | Diarrheic shellfish poisoning | World-wide | White 1988 |
| 1979 | Menhaden kill (red tide) (*Gonyaulax excavata*) | Maine | White 1988 |
| 1979, 1982 | Mass kill of cultured fishes (*Heterosigma akashino*)(red tide) | western Scotland | White 1988 |
| 1979 - present | Chronic outbreaks *Acanthaster planci* | Guam | Birkeland 1989 |
| 1979 - present | widespread death of *Acropora palmata* and *Porites porites* | Anegada, British Virgin Islands | Brown 1987 |
| 1979 - present | Frequency of algal (red tide) blooms in North Sea increases over the last 10 years | North Sea | Saunders 1988 |
| 1979 - present | Isolated incidences of coral reef bleaching of shallow symbiotic hosts | Ko Phuket, Thailand | Brown 1987 |
| 1980 | Caribbean-wide fish kill | Caribbean, Bahamas, Florida (USA) | Williams, E. & Williams 1987 |
| 1980 | Mass mortality of anchovies (*Engraulis mordax*) | Santa Cruz Harbor California, USA | Friedman 1989 |
| 1980 | Fish kill (red tide) (*Gyrodinium aureolum*) | Scotland | White 1988 |
| 1980 - present | Series of red tides | Hong Kong | Wu 1988 |
| Early 1980's | Eelgrass wasting disease | New Hampshire and Maine, USA | Short et al. 1986 |
| 1981 | Mass kill of "sardine-like" species (*Harengula*??) | Venezuelan coast | Atwood PC |
| 1981 | Diadematid urchin mass mortality | Hawaiian Islands | Birkland & Eldredge 1988<br>Choquette PC, Hau PC |

| | | | |
|---|---|---|---|
| 1981 | Mass kill of cultured fishes (*Heterosigma akashino*)(red tide) | Inland Sea of Japan | White 1988 |
| Summer 1982? | Coastal fishes mass mortality | Venezuela | Newspaper |
| Summer 1983 | Sponge mortalities | South Florida, USA | Causey PC |
| Summer 1983 | Mortalities of fish and shellfish (*Prymnesium calthiferum*) | New Zealand | White 1988 |
| 1983 - 1984 | Sea urchin mass mortality (*Diadema antillarum*) | Wider Caribbean | Lessios et al. 1984<br>Lessios 1988b |
| 1983 - present | Mass mortality of sea fans (*Gorgonia* spp.) | Costa Rica Panama, Colombia | Guzman 1984, Guzman PC |
| 1983 - present | Population reduction (*Crassostrea virginica*) | Gulf of Mexico, Mississippi coast | Newspaper |
| 1983 - present | Mysterous ailment of loons (*Gavia immer*) | Gulf and Atlantic coasts of Florida, USA | McIntyre 1989 |
| 1984 | Mass mortality of anchovies, (*Engraulis mordax*) | Santa Cruz Harbor California, USA | Friedman 1989 |
| July 1984, 1985, 1987 | Kills of farmed fish (red tide)(*Gonyaulax excavata*) | Faroe Islands | White 1988 |
| December 1984 | Sea urchin mortality (*Astropyga magnifica*) | Puerto Rico | Williams et al. 1986 |
| 1984, 1985 | Mass kills of caged fish (*Gyrodinium aureolum*)(red tide) | Inland Sea of Japan | White 1988 |
| 1985-1986 1987 | Giant Clam mass mortality | Great Barrier Reef, Australia | Goggin & Lester 1988; Alder & Braley 1989 |
| January 1985 | Sea urchin mortality (*Eucidaris tribuloides*) | Puerto Rico | Williams et al. 1986 |
| 1985 | Coral mortalities due to red tide | Eastern Pacific | Guzman et al. 1988 |
| 1985 | Pearl and Mother-of-pearl oyster mass mortality | Tuamotu Archipelago French Polynesia | Birkland & Eldridge 1988<br>Intes 1988 |
| June 1985, May-June 1986 | Mass mortalities of herring | Alaska | Meyer 1989 |

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|---|---|---|---|
| Summers from 1985 - present? | Brown Tide Mortalities mussels and scallops (*Aureococcus anophagefferens*) | Narragansett Bay<br>Long Island Bays | Anonymous 1989<br>Bricelj 1987 |
| August 1985 | Fish mass mortality (*Harengula* spp.) | Puerto Rico | This paper |
| October 1985 | Secondary die-off (*Diadema antillarum*) | St. Croix | Lessios 1988b |
| November-December 1985 | Secondary die-off (*Diadema antillarum*) | Panama | Lessios 1988b |
| 1985 - 1986 | MSX epizootic in oysters (*Haplosporidium nelsoni*) | east coast USA | Haskin 1987 |
| 1985 - present | Clam mass mortalities (*Perkinsus atlanticus*) | Portugal | Azevedo 1989 |
| 1986 | Fish and shellfish kills (red tide)(*Ptychodiscus brevis*) | Texas (worst ever in Gulf of Mexico) | White 1988 |
| June 1986 | Mass mortality of sea urchins (*Echinometra mathaei*) | Okinawa | Tsuchiya et al. 1987 |
| June 1986 | Mass kill of cultured fishes (*Heterosigma akashino*)(red tide) | British Colombia | White 1988 |
| 1986 - 1989 | 50 beluga whales immuno-deficiency | St. Lawrence River | Goodavage 1989 |
| August 1986 - present? | Sponge epizootic (*Hippospongia communis*) | eastern Mediterranean Tunisia, Greese, Turkey, Cyprus | Reiswig 1988<br>Vicente 1989 |
| October 1986 | Massive fish kill | Texas, USA; Mexico | Associated Press 1986 |
| 1987 - 1989 | Distemper epizootic and mass mortalities of seals | Lake Baikal, USSR | Clapham & Baraff 1989 |
| June 1987 - March 1988 | Bottlenose dolphin mass mortality | Atlantic coast of U.S. New Jersey to Florida | Segars 1987<br>Hollings 1988<br>NOAA 1989<br>Scott et al. 1988<br>Geraci 1989 |
| Summer 1987 | "Enormous" fish kill | Long Island Sound USA | Hollings 1988 |
| Summer 1987 | Shellfish kill, fish kill | Long Island Sound USA | Van Patten 1989 |
| Summer 1987 | Sponge mortalities | south Florida, USA | Causey PC |

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|---|---|---|---|
| Summer 1987 | Mass mortality, commercial oyster (MSX, *Haplosporidium nelsoni*) | Massachusetts to Georgia, USA | Fritz & McVey 1989 |
| August - September 1987 | Epizootic of black band disease | Florida Keys, USA | Causey PC |
| Summer-fall 1987 | Sea grass blight | south Florida, USA | Tasker 1988 |
| Fall 1987 | Mass mortality of fishes | Norway | |
| Fall 1987 | Humpback and Minke Whale die-off (red tide) | New England, USA | White 1989 |
| Fall 1987 | Fish kills (*Harengula* spp.) | St. Kitts/Nevis | This paper |
| November 1987 - July 1988?? | Abalone mortality (black, red, pink, & green abalone) | California, USA | Richards 1988 |
| Autumn/Winter 1987 | Amnesic shellfish poisoning and massive diatom bloom (*Nitzschia pungens*) | Canada, but possibly a world-wide problem | Bird and Wright 1989 |
| September 1987 - February 1988 | Massive red tide (*Ptychodiscus brevis*) | North Carolina | Bonaventura & Bonaventura 1988<br>Tester 1988 |
| January 1988 | Worst red tide in 10 year series (*Gonyaulax polygramma*) | Hong Kong | Wu 1988 |
| 1988 | Red tides increasing in frequency | Kuwait | Linden in Jeftic et al. 1988 |
| 1988 | 7,000 harbor seals distemper epizootic | North Sea | Goodavage 1989 |
| 1988? - Present | Eelgrass wasting disease | North America & Europe | Muehlstein PC |
| 1988 - Present | Blue-green algae overgrowth of turtlegrass | US and British Virgin Islands | Muehlstein PC |
| Mid May - mid June 1988 | Mass mortality (red tide) (*Chrysochromulina polylepis*) | Norway | Saunders 1988 |
| Summer-fall 1988 | Sea grass blight | south Florida, USA | Tasker 1988 |
| Winter 1988 | Fish Kills (*Harengula* spp.) | St. Kitts/Nevis | This paper |

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|---|---|---|---|
| Late 1988 | Amnesic shellfish poisoning and massive diatom bloom (*Nitzschia pungens*) | Canada, but possibly a world-wide problem | Bird and Wright 1989 |
| January - March 1989 | Brown pelican mortality | Puerto Rico and US Virgin Islands | This paper |
| May 1989 | Fish Mass Mortality (*Harengula* spp.) | St. Vicent | Sealy PC |
| June 1989 | Fish Mass Mortality (*Harengula* spp.) | Barbados | Sealy PC |
| Recent | Epidemics [sic] of tumors in soft-shell clams | Massachusets, USA | Smolowitz 1987 |
| In recent years | Disturbing spread of paralytic shellfish poisoning | Worldwide | White 1988 |
| ? | Mass mortality (*Acropora cervicornis*) | San Blas Islands Panama | Knowlton et al. 1988 |
| ? | *Acanthaster planci* outbreaks | Australia | Zann & Moran 1988<br>Endean 1982<br>Walton 1984 |
| ? | Coralivorus gastropod outbreak (*Drupella* sp.) | Miyake-jima (Japan)<br>Phillipines<br>western Australia | Birkland & Eldridge 1988 |
| ? | Mass sponge mortality (*Chondrilla nucula*) | Puerto Rico | Vicente 1989 |
| ? | Black band disease *Pseudopterogorgia acerosa, P. americana*) | Florida Keys, USA | Feingold 1988 |

[1] This table does not represent an exhaustive search for major marine ecological disturbances, only those that came to the attention of the authors during the bleaching study. Most marine mortalities go unreported.

Bunkley-W., 1988, 1989; Table 23), and many of these events were first noticed in the late 1970's or early 1980's (Brown, 1987; Sindermann, 1988; Table 1). The possibility of relationships and shared causes among these events requires examination.

## ALERT AND COMUNICATION CENTER AND NETWORKS

The bleaching episodes of 1979, 1980, 1982, 1983 and 1986 were not immediately recognized as parts of world-wide, circumtropical events because no agency was looking for large scale events. Many of the reports of bleaching in locations other than the eastern Pacific that were published by Glynn (1984a,b) were sent to him unsolicited (Glynn, 1984a). No comprehensive attempt was made to follow these events. Other reports of bleaching, with the exception of Brown (1987), were largely of local events. Major marine ecological disturbances are often misidentified and understudied as local, disjunct events. Possibly, a first step toward recognizing and dealing with large scale events would be an "Alert and Communications Center" where major marine ecological disturbances could be recorded, similar reports collated, and summaries issued. A similar system has been established to follow red tides by Sea Grant and the Woods Hole Oceanographic Institution (White, 1989). A network to follow marine mammal strandings in North America has existed at the Smithsonian Institution since 1975 as the "Scientific Events Alert Network" (1975-1982) and the "Marine Mammal Events Program" (1982-present). A similar program has been proposed in Europe (Cousteau, 1984).

Some time in the late 1970's, 2 of the principal reef-building corals in the shallow Atlantic coral reefs began to die. This mass mortality continued until the majority of *Acropora cervicornis* in the region was destroyed (Carpenter in Hollings, 1988) and *A. palmata* was severely affected. In 1980, fishes died throughout the tropical and subtropical western Atlantic. The disturbance lasted for months and millions of fishes perished (Williams et al., 1982; Atwood, 1984; Williams, E. and Williams, 1987). In 1981, a mass mortality of diadematid sea urchins occurred in the Hawaiian Islands (Choquette PC; Hau PC). We are unaware of any attempts made to follow, document or study these major events. The 1983 greater Caribbean-wide *Diadema antillarum* mass mortality was well followed and documented by Lessios et al. (1983, 1984) and Lessios (1988), the 1982-83 world-wide coral reef bleaching event was followed by Glynn (1984a,b), and the world-wide epizootic ulcerative syndromes of fishes was reviewed by Sindermann (1988), but none of these events has been studied in sufficient detail. No causes have been assigned. Many other related events (Table 23) are probably more serious and widespread than the limited available data suggest. Studies of coral reef host diseases have not been fundable (Shinn, 1989). A recent proposal to examine the MMED of sponges in the mediterranean failed to obtain support (Reutzler PC) and a recent study of white band disease was underfunded to the point of leaving the etiology of the disease unexamined (Peters PC). The recent review of the MMED of *Diadema antillarum* (Lessios, 1988) shows that much work has been accomplished on the ecological aftermath of this epizootic, but nothing is known about the disease. Examination of these diseases may be critical to our understanding of coral reef deterioration and possibly other related largescale MMEDs (Table 23).

The number, complexity, extent and severity of these disturbances is alarming. Our lack of understanding and documentation of the events is a cause for concern. Glynn (1984a), Birkland and Eldredge (1988), Sindermann (1988) and Ogden (1989) have called for more rapid and comprehensive investigation of regional and global MMEDs. We suggest that an Alert and Communications Center (ACC) would be the most inexpensive, elemental and basic start toward confronting these serious disturbances. A simple, but continuing, ACC could provide: (1) Early detection of each event through a "Hot-line" and a communication network for existing field biologists; (2) Confirmation of the extent of the problem by appropriate members of a field network; (3) Study of the event by existing scientists in unaffiliated laboratories who can quickly be notified of a potential disturbance; (4) Communication of progress through summaries based on questionnaires in cooperation with unaffiliated experts. The ACC would function largely with existing field scientists and existing experts who would appreciate and would act upon timely information about major marine ecological disturbances. This useful system could replace the former disarray and dismay in dealing with these major events (Williams, E. and Williams, 1987).

Most information about a major marine ecological disturbance is only available while the event is occurring. Once a disturbance ceases, both interest in reporting the event and the reliability of memory decline. The bulk of the data we obtained to understand the patterns of bleaching in 1986-88, left unrecorded, would have essentially ceased to exist. Without an Alert and Communication Center-type effort, large-scale coral reef bleaching would have remained a mysterious event.

We hope our limited efforts to follow the 1986-88 coral reef bleaching events suggest what more could be accomplished with a permanent, well advertized, Alert and Communication Center. A Center, which would have been called in mid-June 1987 about the impending bleaching event and mortalities in the Florida Keys (Causey PC), could have alerted coral reef scientists then instead of in late October (as actually happened). A Center would not only have been contacted about the 1986 events, but may have been able to accurately predict the 1987-88 event 1 year in advance [whether the model (Fig. 4) is accurate or not, it would, in this case, have made a correct prediction in 1986]. Fisheries biologists in many areas of the Caribbean would not be investigating possibly related mass mortalities of the same species of fish as isolated events (Table 23). Dozens of biologists, who have studied the 1983-84 mass mortalities of *Diadema antillarum* and the effects on Caribbean reefs (Lessios, 1988), would not have been unaware of a similar mass mortality of diadematids which occurred in the Hawaiian Islands in 1981 (Table 23). The discovery of a virus causing a mass mortality of pearl oysters (Birkeland and Eldredge, 1988) would be known to researchers reporting no pathogenic vector for apparently the same event 4 months later (Intes, 1988) (Table 23). And many more pieces (which are now being lost) of each puzzle would be made available for those who seek to solve these problems.

We believe we have found sufficient correlations to implicate the causes of the recent world-wide coral reef bleaching events by using the techniques that would be employed by an Alert and Communications Center. We hope this concept can be used to follow other important MMEDs.

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## PERSONAL COMMUNICATIONS (PC) LIST

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**APPENDIX 1.** The following questionnaire, or a similar version (there were several versions that were sent out by us or reprinted in other publications) was used to gather the information used to make this report. This form may also be used for additional reports to us about coral reef bleaching or mortalities.

## CORAL AND OTHER COELENTERATES AND SPONGES BLEACHING AND MORTALITIES QUESTIONNAIRE

Department of Marine Sciences, Caribbean Aquatic Animal Health Project, University of Puerto Rico,
P.O. Box 579 or 908, Lajas, PR 00667
Telephone (809) 899-2048. Telex: UPR MAY 3452024. FAX: 809-265-2880

Please complete and return as soon as possible. Save or xerox an extra copy to report more than one geographic location, for future observations, or to send to other observers. If an answer requires more space, use the question number, and continue your answer on another sheet of paper. Thank you.

NAME:
ADDRESS:

TELEPHONE NUMBER(S):

TELEX:
FAX:

DATE OF OBSERVATIONS:

DATE QUESTIONNAIRE COMPLETED:

1. Circle the groups which bleached: Stony corals; Fire Corals; Soft corals; Zoanthids; Anemones; Hydroids; Sponges; Mollusks; ____________.

   Please also complete the following form if possible.

| SPECIES BLEACHED | NUMBER SEEN | NUMBER BLEACHED | % SURFACE BLEACHED |
|---|---|---|---|
| | | | |
| | | | |
| | | | |
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| | | | |
| | | | |

2. What percentage of the total area of all living corals in a geographic area were bleached ?

3. Were there patterns of bleaching within geographic areas or habitats?

4. What geographic areas were involved?

5. At what depths did the bleaching occur?

6. What animals (closely related to those that were bleached) were not bleached?

7. When did the bleaching start?

8. What bleached first? What bleached last?

9. What recovered first? What recovered last?

10. When did recovery begin?

11. How long did it take for the bleaching to occur? Days? Weeks? Months?

12. How many whole colonies died? How many suffered partial necrosis?

13. Did mortalities occur during the bleaching? After the bleaching?

14. What do you think caused the bleaching?

15. What bleaching events have occurred before in your geographic area?

16. How do past bleachings compare with the present bleaching?

17. Did more or less bleaching occur in particular habitats or situations?

18. When did the bleaching become the worst or the most extensive?

19. Was geographic spreading of this event observed?

20. Were any unusual physical or meterological events noted before or during the bleaching?

21. Were temperatures and/or other measurements taken at the surface and/or at depth during and/or before the bleaching?

22. Besides the bleached coelenterates and sponges, were any other animals and/or plants noted damaged or killed during the bleaching event?

23. Did anything else out of the ordinary occur during the bleaching?

24. Please add any additional comments or information which you feel are pertinent.

25. What other topics should have been included in this (and future) CAAHP questionnaires?

Thank you very much for this valuable information. Everyone who responds will receive summaries of the information as it becomes available.

**APPENDIX 2:** Classification and authors of names used. Phyla follow Margulis and Schwartz (1988)

- I. Kingdom Prokaryote - Bacteria
  - Phylum Cyanobacteria - Blue-green algae
    - "cyanobacteria"
    - Class Oscillatoriaceae
      - Order Oscillatoriales
        - *Phormidium corallyticum* Ruetzler and Santavy
  - Phylum Pseudomonadia(?)
    - "bacteria"
  - Phylum Omnibacteria(?)
    - "bacteria"
- II. Kingdom Protoctista
  - Phylum Dinoflagellata - Dinoflagellates
    - "dinoflagellate"
    - *Gonyaulax polygramma*
    - *Gonyaulax excavata*
    - *Gyrodinium aureolum*
    - *Ptychodiscus brevis* (Davis)
    - "zooxanthellae"
  - Phylum Haptophyta
    - *Chrysochromulina polylepis*
    - *Prymnesium calithiferum*
  - Phylum Chrysophyta
    - Class Raphidomonadales
      - *Aureococcus anophagefferens*(?)
      - *Chattonella antiqua*
      - *Heterosigma akashino*
  - Phylum Bacillariophyta - Diatoms
    - *Nitzschia pungens*
  - Phylum Rhodophyta - Red Algae
    - "red algae"
    - Class Corallinaceae
      - Order Corallinales
        - "coralline algae"
  - Phylum Ciliophora - Ciliates
    - "ciliate"
  - Phylum Apicomplexa
    - Class Perkinsea
      - Order Perkinsida
        - "perkinsid"
        - *Perkinsus atlanticus* Azevedo
        - *Perkinsus* sp.
    - Class Sporozoasida
      - Order Coccidida
        - "coccidian"
      - Order Haplosporida
        - *Haplosporidium nelsoni* (Haskin, Stauber and Mackin)
- III. Kingdom Fungi - Fungi
  - "fungi"

- IV. Kingdom Animalia - Animals
  - Phylum Porifera - Sponges
    - "unidentified sponges"
    - Class Demospongiae
      - Order Homosclerophorida
        - *Plakortis* sp.
      - Order Carnosa
        - *Chondrilla nucula* Schmidt
      - Order Halichondriida
        - *Hymeniacidon* sp.
      - Order Hadromerida
        - *Anthosigmella varians* (Duchassaing and Michelotti)
        - *Cliona aprica* Pang
      - Order Haplosclerida
        - *Xestospongia muta* (Schmidt)
      - Order Poeciloscierida
        - *Agelas conifer* (Schmidt)
        - *Mycale laevis* (Carter)
      - Order Dictyoceratida
        - *Hippospongia communis* Linnaeus
  - Phylum Cnidaria - Corals and allies
    - "cnidarians"
    - Class Hydrozoa
      - "hydrozoans"
      - Order Milleporina - Fire corals
        - *Millepora alcicornis* Linnaeus
        - *Millepora complanata* Lamarck
        - *Millepora dichotoma* Vaughan
        - *Millepora platyphylla* Ehrenberg
        - *Millepora* sp.
      - Order Stylasterina - Stylaster corals
        - *Stylaster roseus* (Pallas)
    - Class Anthozoa
      - "anthozoid"
      - "anthozoan"
      - Order Helioporacea - Blue coral
        - *Heliopora coerulea* (Pallus)
      - Order Alcyonacea - Soft corals
        - "alcyonarians"
        - *Cladiella* sp.
        - *Lobophytum* sp.
      - Order Gorgonacea - Gorgonians
        - "unidentified soft corals"
        - *Briarium asbestinum* (Pallas)
        - *Eunicia* sp.
        - *Iciligorgia schrammi* Duchassaing
        - *Gorgonia* sp.
        - *Pseudopterogorgia acerosa* (Pallas)
        - *Pseudopterogorgia americana* (Gmelin)
      - Order Actiniaria - Sea Anemones
        - "unidentified anemones"
        - *Stoichactis helianthis* (Ellis)
      - *Order* Corallimorpharia - Coral-like anemones
        - *Ricordia florida* (Duchassaing and Michelotti
      - Order Zoanthidea - Zooanthids
        - *Palythoa caribbea* Duchassaing
        - *Palythoa mammilosa* (Ellis and Solander)

- *Palythoa tuberculosa* Esper

Order Scleractinia - stony corals

- *Acropora cervicornis* (Lamarck)
- *Acropora palmata* (Lamarck)
- *Acropora* sp.
- "acroporids"
- *Agaricia agaricites* (Linnaeus)
- *Agaricia lamarcki* Milne-Edwards and Haime
- *Agaricia* sp.
- *Colpophyllia natans* (Muller)
- *Colpophyllia* sp.
- *Dendrogyra cylindricus* Ehrenberg
- *Diploastrea heliopora* (Lamarck)
- *Diploastrea* sp.
- *Diploria clivosa* (Ellis and Solander)
- *Diploria labyrinthiformis* (Linnaeus)
- *Diploria strigosa* (Dana)
- *Diploria* sp.
- *Eusmilia fastigiata* (Pallas)
- "Faviids"
- *Favia fragum* (Esper)
- *Favia* sp.
- *Favites* sp.
- *Fungia* sp.
- *Goniastrea* sp.
- *Leptoseris* sp.
- *Meandrina meandrites* (Linnaeus)
- *Montastrea annularis* (Ellis and Solander)
- *Montastrea cavernosa* (Linneaus)
- *Montipora* sp.
- *Mycetophyllia lamarckiana* Milne-Edwards
- *Oculina varicosa* Lesueur
- *Pavona clivosa* Verrill
- *Pavona gigantea* Verrill
- *Pavona* sp.
- *Platygyra* sp.
- *Pocillopora damicornis* (Linnaeus)
- *Pocillopora elegans* Dana
- *Pocillopora meandrina* Dana
- *Pocillopora verrucosa* (Ellis and Solander)
- *Pocillopora* sp.
- *Porites astreoides* Lesueur
- *Porites californica* Verrill
- *Porites lobata* Dana
- *Porites porites* (Pallas)
- *Porites* sp.
- *Psammocora stellata* Verrill
- *Seriatopora hystrix* Dana
- *Siderastrea radians* (Pallas)
- *Siderastrea siderea* (Ellis and Solander)
- *Siderastrea* sp.
- *Solenastrea bournoni* Milne-Edwards and Haime
- *Stylophora pistillata* Esper
- *Stylophora* sp.
- *Symphyllia* sp.

Order Antipatharia - Black corals

- "black coral"

- Phylum Ectoprocta - Bryozoans
    - "bryozoans"
- Phylum Mollusca - Mollusks
    - "mollusk"
    - Class Gastropoda - Univalves
        - "gastropod"
        - Order Archaeogastropoda
            - "black, red, pink, green abalone"
        - Order Mesogastropoda
            - *Drupella* sp.
            - *Revitrona caputserpentis* (Linnaeus)
            - *Strombus gigas* Linnaeus
    - Class Pelecypoda - Bivalves
        - Order Filibranchia
            - *Argopecten irradians* (Lamarck)
            - *Crassostrea virginica* (Gmelin)
            - "mussels"
            - *Mya arenaria* Linnaeus
            - *Mytilus edulis* Linnaeus
            - "scallops"
        - Order Eulamellibranchia
            - *Chama* sp.
            - *Tridacna gigas* Linnaeus
            - *Tridacna* sp.
- Phylum Annelida
    - Class Polychaeta - Polychaete worms
        - "polychaete"
- Phylum Echinodermata - Echinoderms
    - "echinoderms"
    - Class Asteroidea - Sea stars
        - Order Spinulosa
            - *Acanthaster planci* (Linnaeus)
            - *Othilia tenuispina* Verrill
            - *Patiria (=Asterina) miniata* Brandt
        - Order Forcipulata
            - *Heliaster kubinijii* Xantus
            - *Piaster* sp.
    - Class Echinoidea - Sea urchins, sand dollars
        - "echinoderms"
        - Order Cidaroidea
            - "urchins"
            - *Astropyga magnifica* Clark
            - *Diadema antillarum* Phillipi
            - "diadematid urchins"
            - *Echinometra mathaei* (de Blainville)
            - *Eucidaris tribuloides* Lamarck
            - *Tripneustes ventricosus* (Lamarck)
    - Class Holothurioidea - Sea cucumbers
        - Order Aspidochirota
            - *Stichopus parvimensis* (Clark)
            - *Stichopus* sp.

Phylum Chordata - Chordates
Class Ascidiacea - sea squirts
"tunicates"
Class Osteichthys - Bony fishes
"fishes"
Order Anguilliformes
"moray eels"
Order Clupeiformes
*Brevoortia tyrannus* (Latrobe)
*Clupea harengus* Linnaeus
*Harengula* sp.
"herring"
*Engraulis mordax* Girard
Order Gasterosteiformes
"trumpetfish"
Order Perciformes
"anemonefish"
*Ammodytes americanus* DeKay
*Seriola quinqueradiata* Temminck and Schlegel
Class Aves - Birds
Order Pelecaniformes - Pelecans
*Pelecanus occidentalis*
Order Gaviiformes - Loons
*Gavia immer*
Class Mammalia - mammals
Order Carnivora
*Phoca sibirica* Gmelin
*Phoca vitulina* Linnaeus
Order Cetacea
*Balaenoptera acutorostrata* Lacepede
*Delphinapterus leucas* (Pallas)
*Megaptera novaeangliae* (Borowski)
*Tursiops truncatus* (Montagu)
V. Kingdom Plantae - Plants
Phylum Angiospermophyta
Class Hydrocheritaceae
Order Butomales
*Thalassia testudinum* Koenig
"sea grasses"
*Zostera marina* Linnaeus