

Response of Hawaiian and other Indo-Pacific reef corals to elevated temperature

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Abstract. Loss of symbiotic zooxanthellae, or “bleaching” is one of the first visible signs of thermal stress. Critical threshold temperatures for coral bleaching vary geographically, but can be expressed universally as fixed increments relative to the historical mean local summer maximum. Bleaching can be induced by short-term exposure (i.e. 1–2 days) at temperature elevations of 3° C to 4° C above normal summer ambient or by long-term exposure (i.e. several weeks) at elevations of 1° C to 2° C. Corals in both tropical and subtropical locations live at temperatures close to their lethal limits during the summer months. Temperature elevations above summer ambient, but still below the bleaching threshold, can impair growth and reproduction. Temperature and light interact synergistically; high light accelerates bleaching caused by elevated temperature. Bleaching susceptibility is correlated with respiration rate. Any factor that increases respiration (such as high incident light) accelerates bleaching at higher temperatures. Ultraviolet (UV) radiation is a detrimental factor associated with solar radiation. Increased UV due to thinning of the earth’s protective ozone layer may aggravate bleaching and mortality caused by global warming. A warming trend in Hawaiian waters has been observed over the past decade. In 1986, 1987 and 1988 Hawaiian corals were perilously close to their bleaching threshold during the summer months, and localized bleachings did occur. In some cases, local warming of surface water on shallow reef flats exceeded this threshold temperature and caused localized coral bleaching. In other cases, heating of large mesoscale eddies in the lee of the larger islands apparently caused wide-scale bleaching of the most sensitive coral species (*Pocillopora meandrina*) to depths of 20 m. A continuation of the warming trend in Hawaii would lead to mass bleachings similar to those observed recently in other geographic locations.

Introduction

“Bleaching,” or the loss of zooxanthellae and their photosynthetic pigments, was originally described by Vaughan (1914) as a stress response of corals resulting from exposure at low tide, salinity reduction or darkness. Recent mass bleaching of reef corals in Panama and the Galapagos Islands (Glynn 1983–1985; Glynn et al. 1988), throughout the Caribbean and the Florida Keys (Jaap 1979, 1985; Hudson 1981; Lasker et al. 1984; Lang et al. 1988; Williams and Bunkley Williams 1988) on Australia’s Great Barrier Reef (Fisk and Done 1985; Harriott 1985; Oliver 1985), southern Japan (Glynn 1984) and Indonesia (Brown 1987; Brown and Suharsono 1990) and subsequent coral mortality has led to concern over the causes and the long term consequences (Williams et al. 1987). Substantial ecological and physiological information related to coral bleaching was compiled over a decade ago as a part of studies concerned with the effects of thermal discharges from power generating stations on coral reefs (Jokiel and Coles 1974; Coles 1975; Coles et al. 1976; Jokiel and Coles 1977; Coles and Jokiel 1977, 1978). The problem of “thermal pollution” of that era has taken on new meaning with the growing concern over the “greenhouse effect” (Ramanathan 1988) and the potential warming of the world’s oceans over the next century. In this regard, our findings were prophetic: “These results indicate that in both tropical and subtropical environments large populations of corals are exposed to temperatures precariously close (within 1° C and 2° C) to their upper lethal limit during the summer months” (Coles et al. 1976, p 162). The purpose of this paper is to summarize and integrate our previous experience with the response of reef corals to elevated temperatures. Further, we will relate these results to the present bleaching problem and possible future bleaching problems on coral reefs associated with global warming.

Temperature and bleaching in reef corals

Yonge and Nicholls (1931) were the first to report coral bleaching as the result of elevated temperature in the field. They performed classic experiments which still stand as the most complete descriptions of zooxanthellae expulsion by corals under thermal stress. The first quantitative measurements of photosynthetic pigmentation

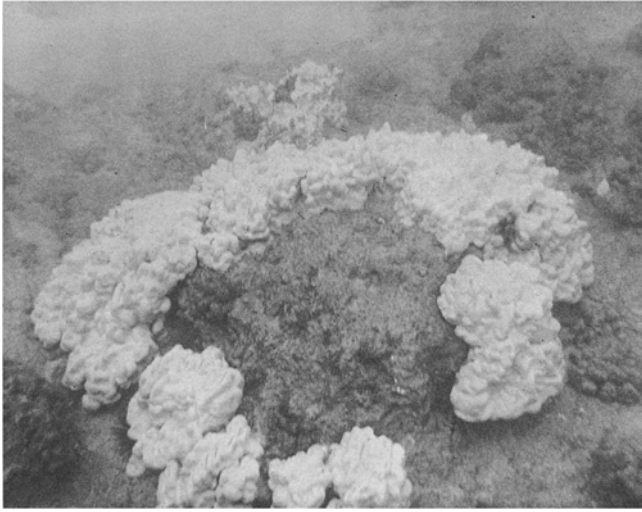


Fig. 1. Surviving massive colony of bleached *Porites lobata* amid dead corals (*Pocillopora meandrina*) in the thermal outfall of the Kahe Power Generating Station, Kahe Point, Oahu during October 1971

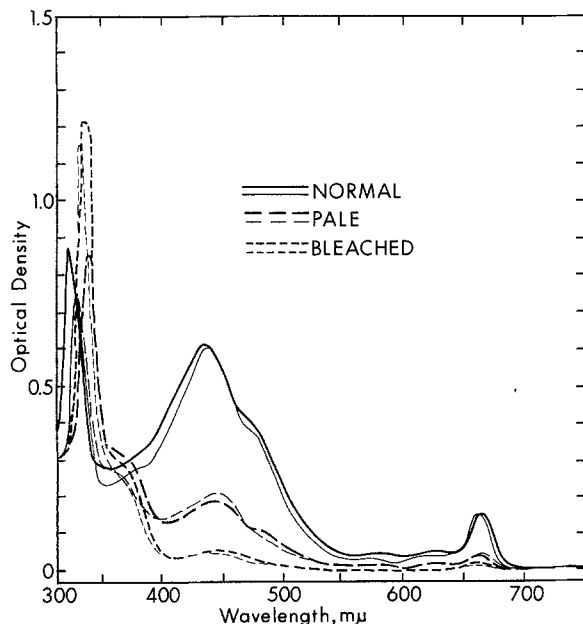


Fig. 2. Absorption spectra for replicate acetone extracts of bleached, pale and normal specimens of the Hawaiian reef coral *Montipora verrucosa*. The 665 nm peak corresponds approximately to chlorophyll *a* concentration; 630 nm to chlorophyll *c* and 480 nm to plant carotenoids. Detailed analysis of pigment changes in bleached corals is contained in Jokiel and Coles (1974)

reduction were performed by Jokiel and Coles (1974) for corals that had been exposed to thermal effluent from a power station in Hawaii (Fig. 1). "Pale" corals (defined as showing visible decreases in pigmentation) showed reductions in chlorophylls *a* and *c* from 1 to 2 orders of magnitude, while "bleached" or totally colorless specimens had extremely low levels of these pigments (Fig. 2). Reduction of pigment per unit area of coral skeleton in reef corals is modified by two mechanisms (Kinzie et al. 1984). Within the normal range of environmental conditions, the non-perforate Hawaiian species *Pocillopora damicornis* appears to decrease pigment by decreasing the cellular concentration of chlorophyll per zooxanthella while *Montipora verrucosa* appears to change the number of zooxanthellae per unit area. Actual mass expulsion of zooxanthellae occurs when temperature is high.

Bleaching can cause varying degrees of coral mortality, depending on the temperature, light regime, species and exposure time (Coles et al. 1976; Jokiel and Coles 1977; Coles and Jokiel 1978). Rate of mortality can vary considerably within and between species, depending on the degree and duration of warming. For example, exposure of 1 to 2 days to 4° C to 5° C above normal summer ambient produces extreme bleaching followed by high rates of mortality (Jokiel and Coles 1977). The same exposure time at 2° C to 3° C above summer ambient temperature results in gradual and less extensive bleaching and lower mortalities of 0% to 10% (Jokiel and Coles 1977; Coles and Jokiel 1978).

Field studies of bleaching supported by accurate in situ temperature records support the above generalizations which are based on investigations under highly controlled experimental conditions. Under field conditions, temperature elevations exceeding 4° C or more produce massive bleaching followed by 90% to 95% mortality (Jones and Randall 1973; Jokiel and Coles 1974; Coles et al. 1976; Neudecker 1981; Glynn 1984; Harriott 1985). Prolonged exposure to temperature elevations as small as 1° C to 2° C above normal summer ambient maxima can produce bleaching, but often with low mortality and rapid recovery of pigment in cooler months (Coles 1975; Coles and Jokiel 1978; Hudson 1981; Jaap 1979, 1985; Lasker 1984).

Bleached corals can recover when temperature conditions return to normal (Yonge and Nicholls 1931). Partial recovery has been observed within one month, and a full return to normal coral pigmentation has been observed within two months after thermal stress was removed (Jokiel and Coles 1974, 1977; Jaap 1979; Hudson 1981). Ability of the corals to recover after bleaching follows the same relative order as initial thermal resistance (Yonge and Nicholls 1931; Jokiel and Coles 1977; Glynn 1983).

Concentrations of zooxanthellae in the bleached coral tissues can be reduced nearly to zero, but sufficient cells generally remain for the coral to recover pigmentation after the stress is removed. We could always detect a few live zooxanthellae with a fluorescence microscope, even in the most highly bleached corals. Perhaps thermally bleached corals can also acquire zooxanthellae by incorporation of planktonic phases of *Symbiodinium microaeriatricum*. Corals that have lost zooxanthellae can regain

them through direct contact with a healthy coral (Franzisket 1970).

Bleaching is not induced by the "thermal shock" of rapidly fluctuating temperatures, but rather is a response to prevailing mean temperature. Corals growing in a power station discharge that showed continual temperature oscillations of 3° C to 4° C every few minutes throughout the year did not bleach during winter when the temperatures were below mean summer ambient maxima (Coles 1975). These corals subsequently lost their pigment in the summer months when temperature exceeded critical mean upper limits. This observation has important implications for corals growing on reef flats, where temperature is highly variable. The prolonged mean temperature is more important than short-term rapid fluctuations in controlling coral bleaching and mortality.

Physiological response

Calcification and growth

Short-term measurements of coral calcification using ⁴⁵Ca technique (Clausen and Roth 1975) and long-term growth experiments based on skeletal weight increase and linear extension under controlled temperature conditions (Jones and Randall 1973; Jokiel and Coles 1977; Houck et al. 1977; Coles and Jokiel 1978) indicate that corals have a growth optimum near the summer temperature maxima. A small prolonged increase of only 1° C to 2° C above this value will reduce skeletal growth (Jokiel and Coles 1977; Coles and Jokiel 1978). Growth reduction at higher than normal summer temperatures has also been verified in the field by Hudson (1981). Calcification rate in the coral *Pocillopora damicornis* shows two calcification peaks, one at approximately 27° C and a second at approximately 31° C (Clausen and Roth 1975). The 27° C peak is more prominent in Hawaiian corals and the 31° C peak predominates in the Enewetak corals.

Photosynthesis and respiration

Photosynthesis (P) to respiration (R) ratio decreases with increasing temperature above normal summer ambient temperature (Coles and Jokiel 1977). Tropical corals measured at Enewetak showed greater photosynthesis (P) to respiration (R) ratio at high temperature compared to subtropical varieties of the same species from Hawaii (Coles and Jokiel 1977). Decreases in the P:R ratio with increase in temperature have been demonstrated in a wide range of other photosynthetic systems (summarized in Coles and Jokiel 1977), suggesting that elevations in temperature above normal summer ambient can result in reduced autotrophic ability at the community level.

The decrease in net production at higher temperature was initially observed in oxygen respirometry on non-acclimated corals (Coles and Jokiel 1977), raising a question as to whether or not corals would eventually acclimate to higher temperature. Controlled experiments in-

volving corals acclimated for 2 months at different temperatures and subsequently measured at those temperatures were conducted (Coles and Jokiel 1978). Mean carbon fixation was substantially lower in the highest temperature treatment (28° C) compared to the treatment approximating summer ambient (26° C). Coral skeletal growth was also lower at the higher temperature.

Synergistic effects between temperature, light and other factors

"We conclude that response of corals to a given ecological factor must vary with changes in other environmental parameters, and that these interactions are most important near the limits of tolerance for a given parameter" (Coles and Jokiel 1978, p 194). Departure of light, salinity or other factors from optimal conditions narrows the range of tolerable temperature and interferes with vital temperature-related physiological mechanisms in reef corals. High natural light intensity accelerated bleaching at high temperature, increased mortality rate, reduced carbon fixation and lowered growth rate (Coles and Jokiel 1978).

Spectrum as well as intensity of solar radiation can influence bleaching. Corals and their contained zooxanthellae are responsive to spectral distribution in the UV (Jokiel and York 1982). Spectral composition in the visible range influences pigmentation and growth in reef corals. Kinzie et al. (1984) grew reef corals under filters that produced fields of similar quantum flux but different spectral composition. Blue or white light promoted pigmentation and growth more than green or red light. Substantial bleaching occurred in corals grown for prolonged periods under red light.

Bleaching and respiration rate

The mechanism regulating numbers of zooxanthellae is not understood, but probably involves feedback mechanisms related to metabolic rates and flux of metabolites between the symbiont and the host. Biochemical reaction rates are temperature dependent. Respiration rate increases more rapidly with temperature than photosynthesis, leading to a lowering of P:R ratio and diminishing autotrophic capacity with increasing temperature (Coles and Jokiel 1977). All available direct evidence indicates that coral bleaching at abnormally high temperatures is correlated with respiratory rate. Species with the highest respiratory rates are most sensitive to bleaching and mortality (Jokiel and Coles 1974; Coles and Jokiel 1977). Interspecific differences in the magnitude of P:R ratio of Hawaiian corals at elevated temperatures correlate with thermal tolerance (Coles and Jokiel 1977). Species that can maintain higher P:R ratios at elevated temperature are more resistant to bleaching and mortality.

These observations lead to the hypothesis that any factor that increases respiration will accelerate bleaching at elevated temperatures. The dark respiration rate of corals increases by as much as 60% after the coral is ex-

posed to 80 minutes of illumination (Edmunds and Spencer-Davies 1988). Increased light intensity eventually leads to "sun adaptation" and a higher rate of respiration (e.g. Chalker et al. 1983; Jokiel and Morrissey 1986). Portions of coral colonies receiving the highest incident radiation bleach more readily than portions that are shaded. Hence, the temperature-light synergism seems to be partially correlated with respiration rate in different parts of the same colony as well as in colonies growing in different light regimes.

The role of UV in the temperature-light synergism (Jokiel et al. 1975; Harriott 1985; Jokiel 1988) should not be discounted, but probably is of less importance than respiration-related effects. Damaging UV radiation can be effectively screened by UV-blocking compounds (Jokiel and York 1984). Also, UV is attenuated more rapidly with increasing depth than visible light.

Ecological considerations

Relative thermal sensitivity of corals

Interspecific differences of Hawaiian corals to elevated temperature were demonstrated in short-term laboratory experiments performed by Edmondson (1928). A similar ranking of Hawaiian species was noted during field studies of corals exposed to heated effluent (Jokiel and Coles 1974). Intraspecific variation in thermal response occurs among different genotypes of the same species. Some coral heads of a given species will remain normally pigmented while adjacent colonies will bleach (e.g. Jokiel and Coles 1974). In the summer of 1988, a number of heads of the coral *Porites compressa* bleached in northern Kaneohe Bay. Ongoing genetic studies suggest that the bleached heads were clone-mates of a genotype that is extremely sensitive to higher temperature (C. Hunter and R. A. Kinzie III, personal communication). Other genotypes of the same species did not bleach.

Reproduction and recruitment of corals at different temperatures

The effect of elevated temperature on recruitment of corals depends on many factors including effect of temperature on production of coral planulae, effect of temperature on the planulae themselves and effect of temperature on settling and on the newly settled corals. Elevated temperature stimulates planula release (Edmondson 1946; Harrigan 1972), but these planulae may be immature and less capable of survival. Planula production of *Pocillopora damicornis* on the Great Barrier Reef was diminished during summer months when temperatures exceeded the thermal optimum for the adult coral (Harriott 1983). Jokiel (1985) found a significant correlation for planula production with temperature for "Type B" *P. damicornis* in Hawaii but not for "Type Y." Physiological differences among different genetic strains of *Pocillopora* are widely cited in the literature (Clausen and Roth 1975; Coles et al. 1976; Coles and Jokiel 1977; Richmond

1985). Fadlallah and Lindo (1988) found contrasting patterns of oogenesis in the coral *Stylophora pistillata* from the Red Sea, Arabian Gulf and Palau that corresponded to different temperature regimes.

The optimal growth temperature for new settlements of *Pocillopora damicornis* in Hawaii (Fig. 3) generally corresponds to the 26°C to 27°C optimum reported for skeletal growth (Clausen and Roth 1975; Jokiel and Coles 1977). Successful recruitment, however, shows a far greater response to temperature (Fig. 4). The reduc-

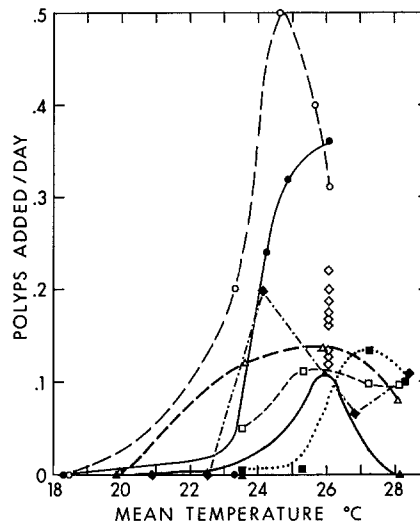


Fig. 3. Effect of temperature on growth of new settlements of the reef coral *Pocillopora damicornis* (Jokiel et al. 1975). Polyps added per day by new settlements at various mean temperatures within various experimental series. Different symbols represent different colonies

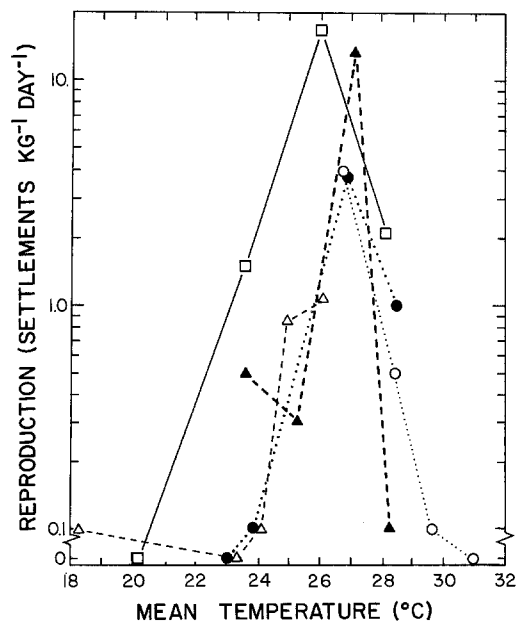


Fig. 4. Effect of temperature on reproduction in the reef coral *Pocillopora damicornis* normalized to biomass of parent corals in microcosm aquaria per unit time (for discussion see Jokiel and Gunther 1978). Different symbols represent different colonies

tion in numbers of settled corals above and below the optimal temperature is an order of magnitude greater than the reduction in growth (Jokiel and Guinther 1978). Recruitment is inhibited at temperatures well below the bleaching threshold.

Planulae appear to be more tolerant of elevated temperature than the adult stages. Edmondson (1946) demonstrated that planulae of *Pocillopora damicornis* and *Cyphastrea ocellina* survive 10 minutes exposure to 40° C and 24 hour exposures to 32° to 33° C. *P. damicornis* planulae tolerate 10 minutes exposure to 10° C above summer maxima with subsequent enhancement of settlement rate and without increased mortality (Coles 1985). Enhanced settlement by higher temperature was also noted by Edmondson (1946) for *C. ocellina*. Increased settlement rate induced by thermal shock of planulae appeared to account for high rates of coral colonization near a thermal outfall (Coles 1984).

Corals as indicators for associated reef biota

Corals can serve as indicators for response of associated organisms and coral reef communities (Jokiel et al. 1975). The thermal ecology of a coral parasite is one example (Jokiel and Townsley 1974). The flatworm *Prosthodinium montiporae* feeds exclusively on the reef coral *Montipora*. This parasite/host relationship appears to be physiologically regulated to allow maximum parasitism under thermal conditions that are optimal for the host. Total weight of parasite production decreased threefold for corals subjected to increases of 2° C over summer ambient. Such thermal regulation of the relationship can produce a seasonably stable parasite/host relationship in areas such as Hawaii where water temperature varies annually between 21° C and 28° C. If other factors remain constant, maximum parasitism will occur when thermal conditions are optimal for the coral, and will diminish under less favorable temperatures. Obviously, such a relationship will produce the maximum parasite biomass over the course of the year with the least damage to the host.

As a second example, "communities" in the square meter by one half meter deep microcosm aquaria used in our controlled temperature experiments showed similar thermal optima and impairment at temperatures above summer ambient (Jokiel et al. 1975). These microcosms developed complex communities during the course of the experiments. Fouling organisms and algae probably recruited from planktonic forms in the continuous supply of sea water, other organisms probably entered inadvertently with the corals. All aquaria were treated in an identical manner except for temperature. At the end of the experiments, all organisms were removed from the microcosms and inventoried. Damage to the corals (bleaching, reduced growth and reduced reproduction) was mirrored in the lowered diversity and biomass of other macrobiota (Jokiel et al. 1975). Data for the macroalgal community (Fig. 5) exemplify these observations. Field studies show similar patterns of increased community damage with increased temperature (e.g. Jokiel and Coles 1974).

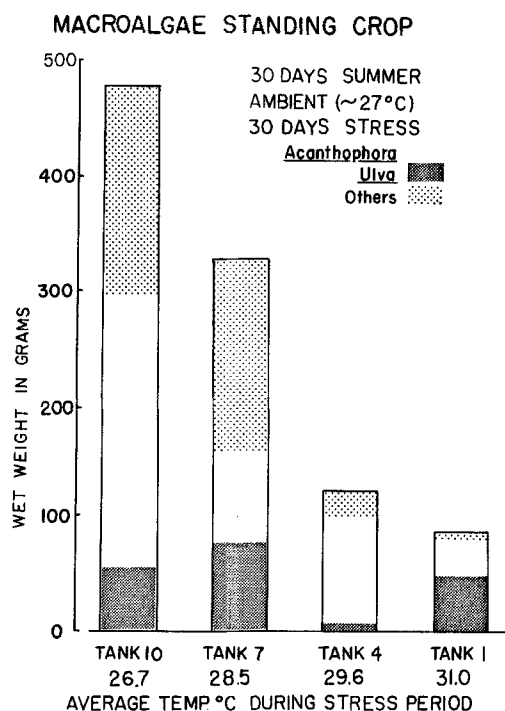


Fig. 5. Standing crop of macroalgae recovered from meter square continuous flow microcosms held at various temperatures (Jokiel et al. 1975)

Geographic variations in lethal temperature

Field observations and controlled experiments in Enewetak and in Hawaii showed that the tropical corals have an upper lethal and sublethal limit that is about 2° C higher than that of subtropical Hawaiian corals (Coles et al. 1976). This difference corresponds to the 2° C difference in normal maximum summer temperature between the two areas. *Porites* from the Florida Keys has a bleaching threshold that is about 1° C higher than for its congener from Hawaii, suggesting adaptation to the higher summer ambient temperatures that occur in Florida (Marcus and Thorhaug 1981). An analysis of sublethal and lethal temperatures and exposure times based on data taken from the classic literature shows that "tropical" *Pocillopora* has a thermal tolerance that is approximately 2° C higher than for "subtropical" *Pocillopora* (Coles et al. 1976). Nowhere is this ability for genetic selection more clearly demonstrated than in the Arabian Gulf, where many species of corals found on offshore reefs tolerate summer maxima of over 34° C for weeks or months without visible change (Coles 1988). The hardiest species survive prolonged exposure to temperatures of 36° C to 38° C on nearshore reefs (Kinsman 1964; Shinn 1972; Coles 1988). These temperatures are well beyond the tolerance determined for corals elsewhere in the world, and may represent the ultimate adaptive limit for scleractinians.

Adaptability of corals to global warming trends

Survival at lethal temperatures can be increased somewhat by pre-exposure to temperatures in the upper sub-

lethal range (Coles and Jokiel 1978). It is likely, however, that local selection over many generations would be required to produce a shift in coral thermal tolerance of local populations. Repeated annual summer bleaching of corals in the thermal plume off Kahe Point, Oahu did not appear to enhance their thermal resistance. The same corals continued to bleach every summer, suggesting that much longer periods of time are needed for adaptation. The possible rate of warming due to the greenhouse effect would probably occur in less than 50 years (Buddemeier and Smith 1988), a time frame that appears to be too short for genetic selection in long-lived reef corals.

The past decade has seen the most dramatic El Niño Southern Oscillation event of this century with resulting high temperature anomalies that caused coral bleaching and mortality on a global basis (Glynn 1984; Brown 1987). The 1980's have already produced the five hottest years on record, with 1988 breaking previous records (Revkin 1988). Warming continues at a time when we would expect temperatures to be decreasing. The solar cycle is in a downturn and dust was thrown high into the atmosphere by the 1982 El Chichon eruption. Both of these factors would tend to decrease global temperatures (Revkin 1988).

A recent trend in ocean warming has been noted in Hawaiian waters (Table 1). A prolonged warming period of this intensity and duration is unprecedented in the long term-record (Seckel and Yong 1977). Summer ocean surface temperatures off Oahu have increased by over 1° C during this time. The warming trend has continued despite record low irradiance (50 year record) observed throughout Hawaii in 1982, which resulted partially from the El Chichon, Mexico eruption (Jokiel 1985). During late summer of 1986 massive bleaching of the most thermally sensitive Hawaiian coral species, *Pocillopora meandrina*, occurred in the southern portion of the Hawaiian Archipelago. Extensive bleaching was reported from lee-

Table 1. Mean temperature of ocean surface waters off Koko Head, Oahu, Hawaii during annual maximum (Sept.-Oct.) for the past 10 years. These data have been taken continuously since 1954 by the Honolulu Laboratory, Southwest Fisheries Center, National Marine Fisheries Service, NOAA (e.g. Seckel and Yong 1977). Data provided by C. Boggs (personal communication). Long term mean for this value from 1954 to 1978 is approximately 26.2°C. Warmer temperatures have continued through the winter and spring of 1989 without an apparent change in the trend

Year	Mean temperature during annual September-October maximum (°C)
1978	26.2
1979	26.6
1980	26.6
1981	26.7
1982	26.5
1983	26.1
1984	26.8
1985	26.8
1986	27.4
1987	27.1
1988	26.9

ward ocean reefs off Olowalu, Maui and Kona, Hawaii to depths of 20 m (J. Naughton and R. Brock, personal communication). Ocean circulation in the Hawaiian Archipelago is variable and dominated by eddies with diameters of from 50 to 150 km (Patzert 1969). Large mesoscale eddies are held in the lee of Maui and Hawaii during the summer months by prevailing current and wind patterns around these large islands (Patzert 1969; Lobel and Robinson 1986). Such gyres persist for many months. The gyres stratify, and solar heating increases temperatures by 1° C to 2° C above the temperature of surrounding surface waters. Satellite infrared photographs clearly show these as large warmwater regions (Lobel and Robinson 1986). These higher temperatures are probably the cause of the observed local bleaching. Ambient oceanic temperature in Hawaii coastal waters exceeded 27° C at that time (Table 1) and a further warming in the mesoscale eddies of 1° C to 2° C would exceed the bleaching threshold of the corals. Warm water in these gyres extends to the 20 m depth of reported coral bleaching. The corals that bleached subsequently recovered full pigmentation during the cooler winter months with low rates of mortality (J. Naughton and R. Brock, personal communication).

Bleaching that results from localized heating in embayments is restricted to shallow water. In late summer of 1987 localized bleaching and tissue loss in *Porites evermanni* was noted on the shallow barrier reef flat off Kaneohe Bay, Oahu and localized bleachings of *Pocillopora damicornis* occurred on lagoon reef flats (G. Hodgson, C. Hunter, J. Stimson, personal communication). The *Porites evermanni* subsequently regenerated tissues and regained pigmentation during the cooler winter months, but the bleached *Pocillopora damicornis* showed high mortality rates. During late summer of 1988 a number of colonies of the coral *Porites compressa* bleached on shallow lagoon patch reefs in Kaneohe Bay, but bleaching was restricted to clones of a few sensitive genotypes (C. Hunter and R. A. Kinzie III, personal communication).

During the summer months of the past few years, Hawaiian corals have been dangerously close to temperature conditions that can produce massive bleaching and mortality. The bleaching threshold was exceeded in localized areas influenced by solar warming of persistent mesoscale eddies and in shallow reef areas having restricted exchange with the open ocean. The next decade will tell us if the observed warming trend is an aberrant fluctuation or the result of global warming.

Although a variety of physical stresses have long been known to induce coral bleaching, elevated temperature appears to be the pervasive factor that resulted in recent mass bleaching phenomena. Unfortunately, temperature data are not available from some of the locations where bleaching events have been noted. Solar radiation accelerates bleaching at high temperatures. This synergism correlates with the effect of visible light acting to increase respiration. The possible threat of bleaching on a global level due to the greenhouse effect could be aggravated by further increases in ambient ultraviolet radiation caused by thinning of the stratospheric ozone layer (Jokiel 1988).

Evidence from the Indo-Pacific region supports the hypothesis that mass coral bleaching could be a harbinger of climatic change. Although firm conclusions would be premature at this point, there is sufficient evidence for serious concern about the environmental implications of these events.

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