Coral Bleaching as an Adaptive Mechanism

A testable hypothesis

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Bleaching in organisms such as hard and soft corals, giant clams, and sea anemones is the loss of pigment associated with their symbiotic algae (zooxanthellae). Bleaching can be the result of loss of the pigmented algae from the host or of loss of pigment from the algae. This article considers only the phenomenon of algal loss. Most attention has been directed to bleaching in scleractinian (hard) corals in the tropics (e.g., Brown 1990, Glynn 1990, Williams and Bunkley-Williams 1990). It is a subject of concern because of mortality and local extinctions associated with large-scale bleaching episodes (Glynn and de Weert 1991; but see Glynn and Feingold 1992), the widespread belief that bleaching episodes have increased dramatically in frequency and intensity within the past decade (D'Elia et al. 1991), and speculation about possible links to global warming (Glynn 1991, Goreau 1990, Williams and Bunkley-Williams 1990).

> **We posit that bleaching allows a host to be repopulated with a different partner**

In this article, we examine briefly some of the salient attributes of bleaching and its biological participants, to which we refer by the names used in the primary literature. We fully realize that these names may not be accurate (see Knowlton et al. 1992 for an example) and that taxonomic precision of both partners is essential for understanding symbioses. We propose a conceptual hypothesis for the role of bleaching in coral reef ecology and evolution that is consistent with most of the available data. We indicate how this hypothesis can be tested, and we discuss its implications for research, management, and conservation.

Acute bleaching is a generalized stress response resulting from a variety of environmental conditions outside the normal local range. It can be induced by stimuli such as unusually high or low temperatures, low light levels or constant light, high levels of UV radiation, salinity shock, and other chemical insults (summarized by, e.g., Cook et al. 1990, D'Elia et al. 1991, Gates 1990), some or all of which may operate synergistically (Coles and Jokiel 1978). Much recent concern has focused on the result of high-temperature stress associated with either the 1982–1983 El Niño event or with the 1987 Caribbean warm event. However, partial or low-level bleaching also occurs in the absence of perceptible stress (Fisk and Done 1985, Gates 1990). Such background bleaching may well have been regarded as an unexceptional feature of coral reef variability before the concern generated by mass bleachings and associated mortality in the middle to latter 1980s (Oliver 1985). Thus, bleaching appears to be a basic physiological attribute of many, if not all, organisms having zooxanthellae, both in response to a variety of stresses and in the absence of obvious stress.

Characteristics of bleaching

Based on published data, we identify three key features of coral bleaching attributed to high temperature:

- The upper temperature limit (beyond which bleaching results) is locally defined: corals may experience local maxima from the mid-20s to the mid-30s degrees C, but at least some corals of most taxa bleach when the temperature rises a few degrees above the local average maximum (Coles et al. 1976, Cook et al. 1990, Jokiel and Coles 1990). Temperature sensitivity is therefore not specific to the coral taxon, but it involves some other component of adaptation.
- There are consistent habitat differences in bleaching resistance at a given locale: corals in habitats that are more variable or more prone to stresses of various sorts, including thermal (such

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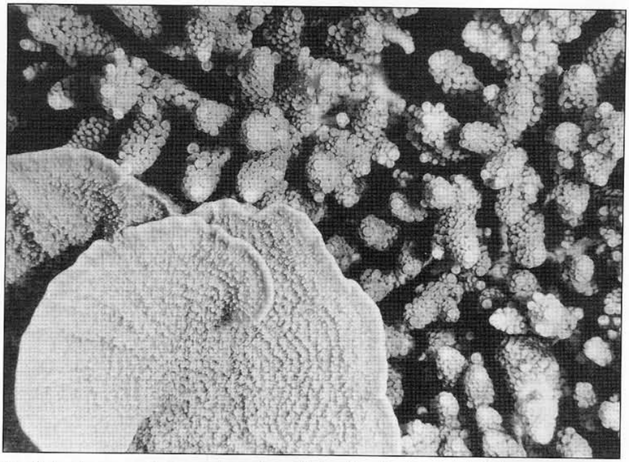
as shallow water or fringing reefs), tend to be less bleached than those in more normally equable environments (Cook et al. 1990, Hoeksema 1991).

- Despite apparent environmental adaptations, there are consistent taxonomic differences in vulnerabilities to stress-related bleaching and in associated mortality at a particular site (e.g., Cook et al. 1990, Hoeksema 1991, Jaap 1985). Prevalence of bleaching appears to be higher in species that have high rates of recruitment and grow rapidly (weedy species) than in other corals in the same general environment (e.g., Gates 1990, Jokiel and Coles 1990, Salvat 1991), and mortality after bleaching is higher in some branching species—particularly members of *Acropora*—than in many massive corals (e.g., Brown and Suharsono 1990, Fisk and Done 1985, Oliver 1985, Salvat 1991). However, intraspecific variability in environmental sensitivity has also been documented, with some but not all sympatric colonies/individuals bleaching (e.g., Brown and Suharsono 1990, Hoeksema 1991, Oliver 1985). Jokiel and Coles (1990) identified temperature-sensitive and temperature-resistant clones of *Porites compressa* in Hawaii.

The underlying assumption in studies of algal symbiosis formerly was that all zooxanthellae belong to *Symbiodinium microadriaticum* Freudenthal, 1962. The evidence for diversity is now overwhelming: biochemical (Ciereszko 1962, 1991, Trench 1971, Von Holt and Von Holt 1968), electrophoretic (Schoenberg and Trench 1980a), morphological (e.g., Blank 1987, Blank and Trench 1985a), and genomic (Rowan and Powers 1991). Whether the algal populations formally are species, races, strains, or ecotypes, their functional distinguishability is adequate to support the hypothesis we advance. We refer to them as *types*. We recognize that our hypothesis would be invalidated by the finding of only one possible combination of host species and algal type as surely as it would be by the existence of a single type of alga in all hosts.

The hypothesis

From the available data on the plant-animal symbiosis, and by analogy with other symbioses (e.g., Fautin 1991) in which partners range from generalists to specialists, we consider it likely that some taxa of hosts and algae can form stable associations with more than one taxon of symbiont. On that basis, we propose that bleaching has the following attributes:



Corals in close proximity such as these Malaysian *Turbinaria* (left foreground) and *Acropora* (background) may host different types of algae. Photo: D. G. Fautin.

- Physiological responses (including those related to stress) of the symbiotic unit are primarily characteristics of the combination, rather than of the host or symbiotic algal partner alone.
- Symbiotic units with one common partner vary in their stress responses and the degree to which they are adapted to different environmental conditions.
- Multiple types of both zooxanthellae and host species are commonly available on reefs.
- Bleaching provides an opportunity for the host to be repopulated with a different type of partner; frequent stress tends to favor a stress-resistant combination.
- Altered environmental conditions (which include altered frequency of stressful events and altered types of stress) favor establishment of combinations of symbionts that were less adaptive under previous conditions.
- Stress-sensitive combinations may have competitive advantages in the absence of stress, which implies gradual reversion to stress-prone but otherwise advantageous symbiotic units in stable environments or in the absence of extreme conditions.

Host-alga symbioses

Symbiont specificity. Uniform, widespread bleaching is uncommon, even among members of a single host species in a particular locale under widespread stress (e.g., Brown and Suharsono 1990, Lang et al. 1988, Salvat 1991), and commonly bleaching occurs only in portions of some colonies (Hayes and Bush 1990, Oliver 1985) or even individuals (Hoeksema 1991). We suggest that at least some of this variation is due to different types of algae in conspecific hosts or even in parts of a genetically uniform host unit.

Schoenberg and Trench (1976, 1980a) found that some species of hosts contain more than one type of zooxanthella; in some cases the host units were sympatric, in others they were geographically separated—but a single individual or colony had algae of only one type. Rowan and Powers (1991) found two restriction fragment length polymorphisms of single-stranded small ribosomal subunit RNA in algae from one of the ten species of reef-forming corals for which multiple samples were examined (as well as in a congeneric species, details for which were not provided), although Rowan[1] doubts that that result is taxonomically significant. Morphological and physiological differences in algae from well-lighted and shaded parts of a cnidarian colony (e.g., Berner et al. 1987 and studies cited therein) may imply multiple types of zooxanthellae, contrary to the usual interpretation of photoadaptation, by analogy with experiments on monocultures of free-living phytoplankters. Level of illumination may be important in defining microhabitats suitable for different types of algae, and thus account for bleaching in corals moved into unfamiliar light regimes (Dustan 1982).

The potential for exchange of symbionts has been demonstrated experimentally: Kinzie and Chee (1979) infected a sea anemone with zooxanthellae from a clam, a nudibranch, and a medusa; Schoenberg and Trench (1980a) infected an anemone with algae from another anemone, a medusa, and three corals; and Fitt (1985) induced production of medusae in scyphozoan polyps with zooxanthellae from 19 other species, including anemones, corals, zoanthids, and clams, and he infected larval clams of two species with algae from anemones and zoanthids. In the field, Schoenberg and Trench (1980a) and Rowan and Powers (1991) found algae of a particular type in hosts belonging to different classes or phyla.

Although many hosts and algae can live with more than one symbiotic partner, there is a spectrum of their abilities to do so. Some types of algae will not establish in heterologous hosts (Schoenberg and Trench 1980b), others establish but do not persist (Kinzie and Chee 1979), and some are a poor physiological fit, as demonstrated by their failure to induce medusa production in scyphozoan polyps (Fitt 1985). Specialists may be more obligate than generalists, the degree of bleaching mortality possibly reflecting the dependence of hosts on their symbionts. For example, the virtually universal mortality of bleached corals of the genus *Acropora* (Salvat 1991) suggests a tightly bound combination.

The range of specificity and stability among partners provides variability on which natural selection can operate and the potential for recombination in the event of mass stress, although we recognize that for a zooxanthella to have one primary preferred host (or even a few) would be a stabilizing community force in the short term. Repopulation following bleaching may result in any of the following: an unstable relationship that breaks down rapidly; a stable relationship in which the alga may be eliminated by competitively superior types over evolutionary/population time scales of the host; an advantageous combination resistant to invasion by other symbionts under nonstress conditions; or coexistence of more than one type, as in the sea anemones *Anthopleura elegantissima* and *Anthopleura xanthogrammica*, which may simultaneously harbor zoochlorellae and zooxanthellae (Muscatine 1971).

Because a symbiotic unit is likely to have attributes possessed by neither partner in isolation (Karakashian and Siegel 1965), we expect a species of coral to vary in stress response with symbiont type and a type of zooxanthella to vary in physiology depending on its host. For any physiological property, assessing the contribution of one symbiont is not a simple matter of subtracting from the value for the intact symbiosis the contribution of the other symbiont measured in isolation. Experiments by Trench (1971), for example, provided preliminary evidence that a particular type of zooxanthella differs biochemically in host corals of various species, and those by Schoenberg and Trench (1976, 1980b) demonstrated that algae of various types differ when grown in genetically identical hosts.

In addition to physiological features of the partners and the combination, we hypothesize that environmental conditions affect specificity. This idea is not new: Kinzie and Chee (1979) pondered whether ecological setting might be more important in explaining features of the symbiosis than identity of the partners. A return to prestress conditions after bleaching may favor restoration of the original symbiotic combination. However, when the stress represents a shift in environmental conditions, the combination is likely to change, if for no other reason than the pre-existing combination experienced those conditions as stressful. Laboratory studies demonstrating that homologous algae displace experimentally introduced heterologous ones (Fitt 1985) illustrate precisely this characteristic, for the experimental setting is manipulated to approximate favorable natural conditions, which are those of the pre-existing symbiotic unit. Frequency of episodic stress will also affect which combination (or combinations) persists, because reversion is rarely instantaneous.

Bleaching mechanism. How bleaching occurs is poorly understood. From laboratory experiments on a coral and a sea anemone exposed to low-temperature shock, Gates et al. (1992) inferred a breakdown in host-cell adhesion. It is unknown how general this mechanism is across taxa of hosts and types of algae, or how it relates to duration and intensity of stress. Complete sloughing of the endodermal cells in which zooxanthellae lodge seems to us pathological, and therefore unlikely to account for the reversible bleaching that appears characteristic of many corals. We believe that in some hosts or under some stresses, the mechanism of loss/regulation is probably less violent and the mechanism of Gates and colleagues may operate primarily in taxa with high mortality rates attendant upon bleaching or in cases of severe stress. Alternatively, some host species may be more tolerant of such damage. Our hypothesis does not depend on a particular mechanism nor on a determination of whether the host (as is commonly assumed) or algal partner initiates bleaching.

Mechanisms of infection and algal spread. Our hypothesis requires that free-living zooxanthellae (swarmers) be available as colonizers. They presumably must be conveyed through water, although, given that densities in seawater are low, vectors such as crustaceans or fish may be important (Fitt 1984, Muller Parker 1984). Detailed predictions based on our hypothesis will differ depending on whether the process of bleaching renders either partner temporarily or permanently unable to form a symbiosis, and whether swarmers are affected by

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[1] R. Rowan, 1992, personal communication. Australian Institute of Marine Science, Townsville, Queensland, Australia.

stress similarly to the same type of alga in a symbiotic unit.

We infer that the repetitive nature of small-scale bleachings (Jokiel and Coles 1990) reflects a lack of reassortment in symbiotic partners. If the types in the water are taxonomically the same as those in the symbiotic population, odds are high that a localized/mild bleaching will produce reinfection with the type of zooxanthella the host had before. Alternatively, reinfection by the same type may be due to "sufficient cells generally remain[ing] for the coral to recover pigmentation after the stress is removed" (Jokiel and Coles 1990, p. 156). The more severe the bleaching, the less likely the latter mechanism and the greater the variety of symbiotic taxa likely to be affected, so the more likely corals are to be repopulated by algae from the external environment (Hayes and Bush 1990), resulting in a higher probability of change.

Repopulation is unlikely to be entirely random. Some combinations of host and symbiont are not viable (Fitt 1985, Schoenberg and Trench 1980b). Thus, the original combination—which, ipso facto, is viable—has a higher-than-random probability of being re-established, particularly if conditions return to prestress levels.

However, to the extent that the alga is rendered incapable of infection by bleaching or that the stress persists, repopulation by a different type is more likely. The factors that govern the types of zooxanthellae in an area may be analogous to the factors thought to govern the diversity of corals on a reef (Oliver 1985): weedy species tend to dominate in the short term but their vulnerability to stress eliminates them disproportionately, checking their number and areal extent and allowing survival of those that grow more slowly but are more stress resistant.

Indeed, Fitt (1985) found that hosts of faster-growing algal types grow faster themselves; if rapid growth is associated with vulnerability to stress, then fast-growing types would readily establish but be subject to repeated bleaching. Reinfection, whether by the original or by another type (or types) of alga, may be facilitated by the attraction of motile zooxanthellae to an aposymbiotic host (a normally symbiotic individual lacking algae) but not to symbiotic hosts (Fitt 1984).

Factors determining which types of algae and how many of each survive may include, in addition to external environment, physiological compatibility, initial numbers, and growth and reproductive rates (probably varying with host species or microhabitat within host). Elimination through alga-alga competition is known among chlorellae (Rahat 1985), and Fitt (1985) showed such elimination for zooxanthellae: in clams, those of a faster-growing type (isolated from a sea anemone) gradually overwhelmed algae of a slower-growing type (isolated from a zoanthid). However, subtle differences in the microhabitats of various parts of a host might favor different types of algae, resulting in a mosaic or chimera, an effect that would be absent in controlled laboratory experiments. (In a chimera, what stresses one type of alga might not stress another, allowing the resistant one to remain and dominate the host after bleaching.)

We consider partial, background bleaching to be not pathological, but rather a normal regulatory process that maintains remarkably stable populations of symbiotic algae despite reproductive potential greatly in excess of that of their hosts (e.g., Muscatine et al. 1985). It may also provide an important route of entry for zooxanthellae under nonstress conditions. This mechanism permits continuous sampling of ambient algae, the fittest ones of which can spread to areas already populated by algae that are either identical or less competitive.

We infer from empirical evidence of repetitive bleaching that algae in a stress-resistant symbiotic unit may be gradually displaced by a less stress-resistant type of zooxanthella that is, in at least some symbiotic associations, better adapted in other ways. For example, combinations with the highest individual or combined growth rate may not necessarily be the fittest in all respects: anemones "infected with homologous algae achieve a somewhat larger biomass but produce fewer offspring than polyps infected with [heterologous] zooxanthellae" (Kinzie and Chee 1979, p. 324). Reversion to the symbiotic unit existing before bleaching is most likely if large populations of the host exist, if intervals between bleaching events are long compared with the time required for reversion, and if the environment returns to its prestress state. The resulting advantageous but vulnerable relationship is episodically disrupted by relatively rare extreme events.

Research needs

There is increasing interest in attempting to define coral and reef community responses to rising temperature and other environmental stresses. Experimentally induced bleaching and predictions of stress response are inconclusive in the absence of definitive taxonomy of both symbiotic partners and some knowledge about the distributions, abundances, and diversity of taxa or types in nature. It is important to resolve these taxonomic and ecological issues before committing extensive resources to field or laboratory studies of inadequately characterized systems.

The hypothesis we advance bears directly on these issues and can be verified or refuted, in part or in the whole, by technically feasible experiments. Regardless of outcome, the research we suggest would provide a conceptually unified approach to a multifaceted subject.

Symbiont specificity within individual coral colonies and in different colonies of the same host species should be investigated in a range of sensitive and robust symbiotic units, as well as in diverse geographic locations. Within-colony studies should focus on corals with characteristics possibly indicative of internal algal diversity—for example, recent or repeated partial bleaching, variations in pigmentation or light exposure, and multiple growth forms (e.g., a massive colony with a platy skirt). Between-colony comparisons should pursue local host differences in habitat, timing of reproduction, seasonality of skeletal density band formation (Lough and Barnes 1990), depth, colony morphology and growth rate (Barnes and Lough 1989), pigmentation, or empirically observed stress resistance. If algal symbiont type can influence skeletal architecture, taxonomic problems in genera where species are difficult to separate conclusively on the basis of skeletal morphology (e.g., Knowlton

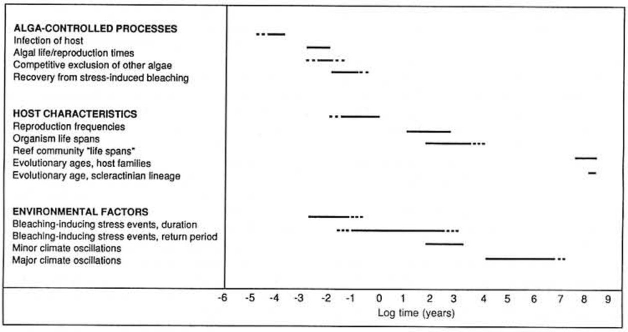

Figure 1. Time scales relevant to bleaching-induced adaptation. Bleaching and infection mechanisms operate at time scales characteristic of the motile and short-lived algal symbionts. These time scales are short compared with host organism time constants and most environmental variation. The symbiotic unit is thereby able to adapt to stress and changes over time scales both longer and shorter than host lifetimes. The punctuated adaptation produced by reshuffling symbionts results in a high level of apparent evolutionary stability for a relatively specialized and apparently fragile organism. Dashed lines indicate possible but not probable extensions of the ranges.

et al. 1992) may be easier to understand. Because the biogeography and ecology of zooxanthella types is essentially unknown, it would be desirable to replicate these studies over large latitudinal and longitudinal ranges.

Surveys to determine the density, variety, and infectivity of swarmers should be done in various localities that differ in dominant symbiotic organisms, and surveys should also be done through time (e.g., seasonally) at those same sites. It would be especially instructive to compare free-living zooxanthellae populations during or immediately after a bleaching episode with those during normal circumstances.

Laboratory studies on stress responses (especially to temperature) of various types of free-living zooxanthellae are necessary to test our hypothesis. These studies should investigate not only viability but also effects on reproduction, photosynthesis and respiration, infectivity, and biochemical products.

We need to know the hierarchy of host species preference by various zooxanthella types and vice versa, and how this hierarchy may vary with environmental parameters. Studies must include the complete spectrum of reef-dwelling symbiotic units, because scleractinian corals may acquire zooxanthellae from host organisms of other taxa. Some symbiotic combinations may be obligate, whereas the physiological bond of others may be looser. Determination of preferences/hierarchies will complement information on the extent to which displacement of one algal type by another occurs.

Empirical studies of stability and physiological features of various coral-alga partnerships should be accompanied by laboratory experiments on variability in stress responses. These experiments should address both naturally occurring symbiotic combinations and deliberate cross-infections and should investigate variability in competitive interactions among algal types under various conditions, expanding on work such as that by Kinzie and Chee (1979), Fitt and Trench (1981), and Fitt (1985).

Our hypothesis has implications for applied research. It suggests that ecosystem management and restoration could become simpler and more effective if resistance to stress can be enhanced by manipulating populations of algae instead of the larger and slower-growing hosts.

Finally, although not integral to our hypothesis, we suggest testing the possibility that stress induces release of biochemical products (e.g., number, type, condition, or effluvia of expelled zooxanthellae) that may act above some threshold as a signal analogous to the alarm pheromone anthopleurine (Howe and Sheikh 1975). A mechanism for propagating mass bleachings beyond the effect of a major primary stress (e.g., to greater depth or protected sites) would help to explain the puzzling local distribution of some bleaching events. If the algae precipitate the bleaching, they could benefit by increasing the diversity or number of available hosts into which to settle. Alternatively, if the hosts were responsible for eliminating their algae, they could benefit by increasing the diversity or density of potential symbionts in the water. Chemosensory attraction has been implicated in the infection process (Fitt 1984).

Evolutionary and ecological implications

Except for the Merulinidae, all currently extant families of reef-forming corals had evolved by the Miocene (and most are Mesozoic in age; Wells 1956). Most corals have lifetimes on the order of decades (centuries in the case of some species), but during the Quaternary, reef environments have repeatedly undergone rapid climate-induced environmental changes on time scales of centuries to millennia (Figure 1). Under these conditions, the fact that the coral lineages have experienced neither rapid taxonomic diversification nor substantial extinctions (Wells 1956) is perhaps unexpected, and the reasons may prove relevant to present concerns about the effects of greenhouse effect–induced climate change (Smith and Buddemeier 1992).

The rapid potential generation time of zooxanthellae compared with that of most hosts might appear to make them (and hence their symbiotic units) evolutionarily more responsive to local conditions than the hosts. However, a sexual phase is unknown for zooxanthellae (Blank and Trench 1985b), which calls into question their potential evolutionary responsiveness. The probable evolutionary stasis of both host and symbiont may be compensated for by the creation of new symbiotic units through recombining symbiotic partners.

We view bleaching as providing an opportunity for reshuffling, a potent adaptive mechanism that instantly creates a host-symbiont combination with features that may prove more robust under altered conditions. Such a mechanism of adaptation, which Saffo (1992) considered as indirectly affecting evolution, could account not only for currently observed local and regional variations in sensitivity to stress of nominally identical host species, but also for the remarkable robustness of coral species and reef community structure throughout the climatic oscillations of the Quaternary.

Time scales of some environmental variations are comparable to those of background cross-infection and competitive elimination of algae from a host (Figure 1). Therefore, the heterogeneity of algae in a host at any time reflects some combination of competitiveness of the algae, time since the most recent stress, frequency of stress, and local diversity of zooxanthellae. Rapid environmental change may thereby produce punctuated adaptation of the symbiotic units, which has been neglected as a subject of study because of the tendency to ascribe stable attributes to the host species as a unitary entity.

Rather than an absence of specificity between partners, our hypothesis posits that specificity changes as environmental conditions do. Thus, although bleaching may represent instability in the short term, it promotes long-term stability by enhancing survival chances of both zooxanthellae and hosts under conditions that are not those of the prestress environment. Potential hosts and habitats are many, so the combination of environmental variability and symbiotic adaptation acts to conserve both genetic and symbiotic diversity.

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