Review

Coral bleaching—how and why?

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Abstract

Bleaching refers to the loss of colour in symbioses between dinoflagellate algae of the genus *Symbiodinium* and marine benthic animals, e.g. corals. Bleaching generally results in depressed growth and increased mortality, and it can be considered as a deleterious physiological response or ailment. An explanatory framework for the causes of bleaching comprises three elements: the external factors or triggers of bleaching, e.g. elevated temperature; the symptoms, including elimination of algal cells and loss of algal pigment; and the mechanisms, which define the response of the symbiosis to the triggers, resulting in the observed symptoms. The extent to which bleaching in different symbioses and in response to different triggers involves common mechanisms is currently unknown, but a contribution of interactions between the algal and animal partners to bleaching is predicted. Symbioses vary in their susceptibility to bleaching as a result of genetic variation in *Symbiodinium* and acclimatory responses of the animal. The evolutionary explanation for bleaching is obscure. Perhaps, bleaching was of selective advantage to the animal hosts under different (more benign?) environmental conditions than the present, or bleaching may be a negative by-product of an otherwise advantageous symbiotic trait, such as the elimination of damaged algal cells.
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Keywords: Adaptive bleaching hypothesis; Coral bleaching; Corals; *Symbiodinium*; Symbiosis; Zooxanthellae

1. Introduction

Everyone knows about coral bleaching. It has been discussed in the soap opera *Neighbors* (or so I am told) and, more seriously, it is recognised widely as a factor damaging the already fragile economies of various developing countries and livelihood of their peoples. Marine biologists have played a crucial role in achieving this awareness, by well-organised and publicised monitoring of bleaching events. Bleaching events are increasing in frequency and severity (Wilkinson, 1999), and the ecological collapse of the world's reefs is predicted by simulation models using current data on the incidence of bleaching and projected climate change (Hoegh-Guldberg, 1999; Risk, 1999).

What should be done? Should we attempt to influence the incidence and scale of bleaching events as part of reef management strategy and, if so, what interventions should be made? Or are the causes of coral bleaching and the actions required to reduce its incidence entirely at a scale far larger than the remit of the coral biologist?

Answers to these questions will require extended dialogue between multiple disciplines, including those with expertise in reef management, coral ecology and the fundamentals of the *Symbiodinium* symbiosis.

The purpose of this article is to provide some input to the dialogue from the perspective of the symbiosis. The key issues from this perspective are (1) the causes of bleaching; (2) the reasons for variation in susceptibility to bleaching; and (3) why, at the evolutionary level, corals bleach. They are addressed in turn, after a brief introduction to the defining features of bleaching. For general reviews of coral bleaching, including comprehensive surveys of the burgeoning literature, the reader is referred to Glynn (1993), Brown (1997) and Hoegh-Guldberg (1999).

2. What is bleaching?

Coral bleaching is a misnomer. Bleaching is not restricted to corals, but displayed by all animals in symbiosis with dinoflagellate algae of the genus *Symbiodinium*, also known as zooxanthellae because of their yellow–brown colour. This symbiosis is restricted largely to

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benthic animals of the phylum Cnidaria (e.g. sea anemones, zoanthids, scleractinian corals and octocorals) in the photic zone at low latitudes, but it is also borne, for example, by some sponges and the tridacnid clams.

Bleaching is defined as the loss of colour, arising from the partial to total elimination of the *Symbiodinium* population or degradation of algal pigments. *Symbiodinium* species possess chlorophyll *a* and c_2, plus various carotenoids, particularly the peridinins which confer the brown colour. In Cnidaria, the *Symbiodinium* cells are generally intracellular, located in cells of the endoderm (one of the two cell layers of the animal) and their elimination arises either from expulsion from the cell or from cell death accompanied, under some circumstances, by expulsion.

Unless the animal tissues are heavily pigmented, the living tissues in a bleached symbiosis are transparent or translucent. Bleached corals are white, the colour of the underlying skeleton of calcium carbonate. The animal partner may survive and the symbiosis recover over a period of weeks to months or, alternatively, the animal tissues may die. The corals and other symbiotic species on some reefs have suffered mass mortality as a consequence of a bleaching event (e.g. Wilkinson, 1999).

The dramatic rise in the incidence and severity of bleaching over the last two decades has led to the perception that bleaching is fundamentally an 'unnatural' phenomenon (e.g. Veron, 1986; Rosenberg and Ben-Haim, 2002) to be contrasted with the 'natural' stable symbiosis. However, symbioses generally display seasonal variation in the density and pigment content of algal cells, with minimal values at the end of the season with the highest sea water temperatures (e.g. Dykens and Shick, 1984; Brown et al., 1995; Stimson, 1997; Fitt et al., 2000). The longer the season of high sea water temperature and the higher the maximum temperatures, the more bleached symbioses with *Symbiodinium* are predicted to become.

3. The causes of bleaching

There is no coherent, simple explanation of the causes of bleaching, despite the considerable research on this topic. An explanatory framework of bleaching proposed in Fig. 1 may contribute to the organisation of available information and to a more precise definition of unresolved problems. Causation can be considered as three elements: the external factors which trigger bleaching;
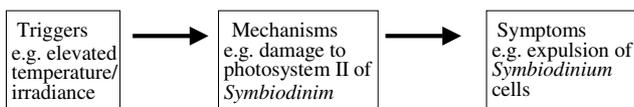
the symptoms which give rise to the observed bleaching; and, at the core of the causes of bleaching, the mechanisms, i.e. the fundamental processes defining the response of the symbiosis to the bleaching triggers and resulting in the observed symptoms. These three elements are now considered in turn.

3.1. The triggers of bleaching

In the laboratory, bleaching can be triggered by multiple factors: extremes of temperature (heat shock and cold shock), high irradiance, prolonged darkness, heavy metals (especially copper and cadmium) and pathogenic micro-organisms [reviewed in Hoegh-Guldberg (1999), Brown (2000) and Ben-Haim and Rosenberg (2002)]. The recent, large-scale bleaching events on the world's reefs have been attributed principally to elevated sea water temperature, often combined with increased solar radiation, and they have been linked to long-term changes in global climate, compounded by El Niño events (e.g. Stone et al., 1999; Walther et al., 2002). Chronic pollution and pathogenic micro-organisms may act synergistically with these abiotic factors. For example, the virulence of the bacterium *Vibrio shiloi*, the causative agent of bleaching in the coral *Oculina patagonica*, is strongly temperature dependent, requiring temperatures $\geqslant 25$ °C (Banin et al., 2001a).

3.2. The symptoms of bleaching

Bleached symbioses in the laboratory and field generally have reduced densities of *Symbiodinium*. Corals which appear completely bleached to the naked eye have experienced a 70 to >90% reduction in algal density (e.g. Fitt et al., 2000) and, in the laboratory, the symptoms at the cellular level giving rise to this condition include the expulsion of algal cells and the detachment and loss of animal cells and their complement of algal cells (Gates et al., 1992; Brown et al., 1995). A key issue to our understanding of bleaching is the extent to which the external factors triggering bleaching determine the symptoms of bleaching. How uniform are the bleaching symptoms displayed by different animal/*Symbiodinium* taxa in response to one factor, and do the symptoms exhibited by a single symbiosis vary between the different triggering factors? These twin questions can be answered empirically, and they should contribute to our understanding of the mechanisms of bleaching, the central and crucial element to the explanatory framework in Fig. 1.

3.3. The mechanisms of bleaching

The information available on the mechanisms of bleaching is fragmentary, like the occasional pieces in a

Fig. 1. An explanatory framework to describe the causes of bleaching.

jigsaw puzzle depicting an unknown picture. The fragments include:

- the damage and reduction in the D1 protein of photosystem II reaction centre of *Symbiodinium* cells (Warner et al., 1999) and disruption to the Calvin cycle mediating photosynthetic fixation of carbon dioxide (Jones et al., 1998), each of which has been suggested to contribute to the mechanism of bleaching in response to elevated temperature and irradiance;
- inhibition of photosynthesis by *Symbiodinium* cells in response to a toxin produced by the pathogen *Vibrio shiloi* (Banin et al., 2001b);
- changes in the cellular patterns of protein phosphorylation leading to the symptom of animal cell detachment (Sawyer and Muscatine, 2001); and
- elements of the necrotic and programmed cell death pathways mediating lysis (Dunn et al., 2002).

These various phenomena are not necessarily mutually exclusive. They may occur sequentially or in parallel, and vary in importance depending on the trigger of bleaching. Future research should not only identify and characterise these and other components of the mechanisms of bleaching but also elucidate their interactions, to yield the network of molecular and biochemical events that define the bleaching mechanisms. In this context, there is a valid place for model symbioses maintained under defined conditions and exposed to triggers of bleaching that may not relate precisely to the triggers of greatest importance in the field.

It is self-evident that the bleaching mechanisms cannot be identical in response to different triggers. For example, prolonged darkness causes bleaching without direct damage to photosystem II of the *Symbiodinium* cells. What is not clear is whether bleaching in response to different triggers and occurring in different symbioses involve common mechanistic components. If there are no universal elements to the mechanisms of bleaching, then bleaching becomes an 'umbrella' term for several or multiple disparate syndromes; to pursue the jigsaw metaphor used above, studying the mechanisms of bleaching would be like trying to solve more than one puzzle simultaneously.

The mechanisms of bleaching are anticipated to involve symbiotic interactions between the algal and animal cells. In the non-bleaching symbiosis, the apparently harmonious persistence, growth and division of the animal and algal cells are underlain by the exchange of nutrients between the partners, including the translocation of substantial amounts of photosynthetically fixed carbon from the algal cells to the animal (Trench, 1993) and a predicted (but unexplored) parallel exchange of signalling molecules. In the bleaching symbiosis, the algal cells are metabolically compromised, with a diminished capacity to provide the animal with photo-
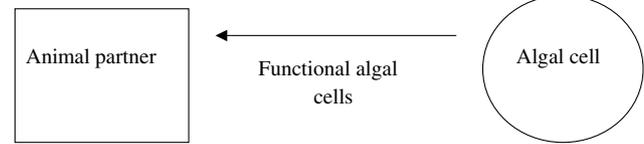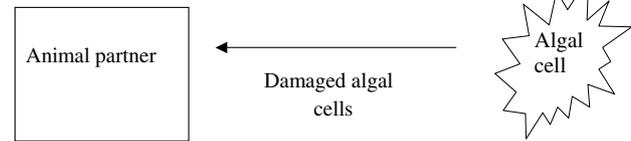

Fig. 2. Alternative mechanisms by which interactions between the partners in the symbiosis may determine whether the symbiosis bleaches (see text for details).

synthetic carbon (Perez et al., 2001). This raises the possibility that the symbiosis is maintained by the sustained production by the algal cells of a signal that inactivates the animal defence responses to foreign organisms, and the loss of this signal leads to bleaching (Fig. 2a). A candidate for this putative signal is the receipt of algal-derived photosynthate by the animal; in the analogous symbiosis between *Chlorella* and hydra (a freshwater Cnidarian), *Chlorella* cells with low rates of photosynthate release are expelled from the symbiosis at elevated rates (Douglas and Smith, 1984). Alternatively or additionally, *Symbiodinium* cells metabolically unbalanced by a trigger of bleaching may release specific compounds or display relatively uncontrolled leakage of cytoplasmic contents, to which the animal partners responds defensively (Fig. 2b). These scenarios raise two possibilities: that the mechanisms and symptoms of bleaching include parallels with the response of Cnidaria to potential pathogens; and that specific algal signals to the animal (or the collapse of these signals) are the common elements in the mechanisms of bleaching in response to all triggers.

4. Variation in susceptibility to bleaching

Symbioses with *Symbiodinium* species are not uniformly susceptible to bleaching. Monitoring of natural bleaching events has revealed marked interspecific and intraspecific variation in the degree of bleaching at one site. For example, among corals, branching forms, e.g. *Acropora* and *Pocillopora* species, generally bleach more strongly than massive corals (e.g. Jiménez, 2001; McClanahan et al., 2001). The determinants of this variation in bleaching susceptibility have been investigated from two perspectives: the molecular ecology of *Symbiodinium* and the ecophysiology of corals.

4.1. Genetic variation in bleaching susceptibility of Symbiodinium

The genus *Symbiodinium* includes considerable molecular variation at the level of the ribosomal RNA genes. It comprises two clades, one known as phylotype A and the other including phylotypes B–F (Rowan, 1998; Wilcox, 1998; Lajeunesse, 2001). Ribotypes A, B and C are cosmopolitan, being widely distributed throughout the Atlantic and Indo-Pacific provinces, although ribotype C is rare and possibly absent from high latitude (>35–40°) sites (e.g. Baker and Rowan, 1997; Savage et al., 2002).

Genetic variation in the susceptibility of *Symbiodinium* to bleaching is strongly indicated by the field study of Rowan et al. (1997) on the closely related corals *Montastraea annularis* and *M. faveolata* on the Caribbean coast of Panama. These species bear *Symbiodinium* of ribotypes A, B and C. Among coral colonies containing both of ribotype B and ribotype C, those with algal populations dominated by B (>80% of the algal cells) did not display bleaching detectable by eye in response to the elevated temperature/irradiance conditions in late summer 1995, and those with algal populations comprising 35% or more of ribotype C became pale or bleached (Fig. 3a). Furthermore, algal cells of ribotype C declined in number disproportionately during bleaching, in colonies containing mixtures of ribotype C and A and/or B (Fig. 3b). The most parsimonious interpretation of these data is that cells of ribotype C in *Montastraea* species have a lower tolerance than ribotypes A and B to elevated temperature/irradiance, and that this difference can account for the observed intraspecific variation in bleaching susceptibility. The biochemical basis of the variation among genetically distinct *Symbiodinium* cells in susceptibility to bleaching is unknown.

Consistent with the results of the study of Rowan et al. (1997), the complement of *Symbiodinium* is altered in some coral species on recovery from bleaching; for example, replacing ribotypes B and C by ribotype A in the *Montastraea annularis* species complex (Toller et al., 2001a) and replacing ribotype C by ribotype D in *Pocillopora damicornis* on the west coast of Panama (Glynn et al., 2001). Ribotypes A and D are retained for at least 9–12 months in these studies; data over longer time scales are not available.

These studies should not, however, be interpreted as evidence that all *Symbiodinium* of ribotype C in all host species is invariably more susceptible to bleaching and replacement other ribotypes. For many reef communities, there is no simple correlation between the bleaching susceptibility of a species and the ribotype of its algal cells; for many animal species, the ribotype of the complement of *Symbiodinium* post-recovery is the same as prior to bleaching.
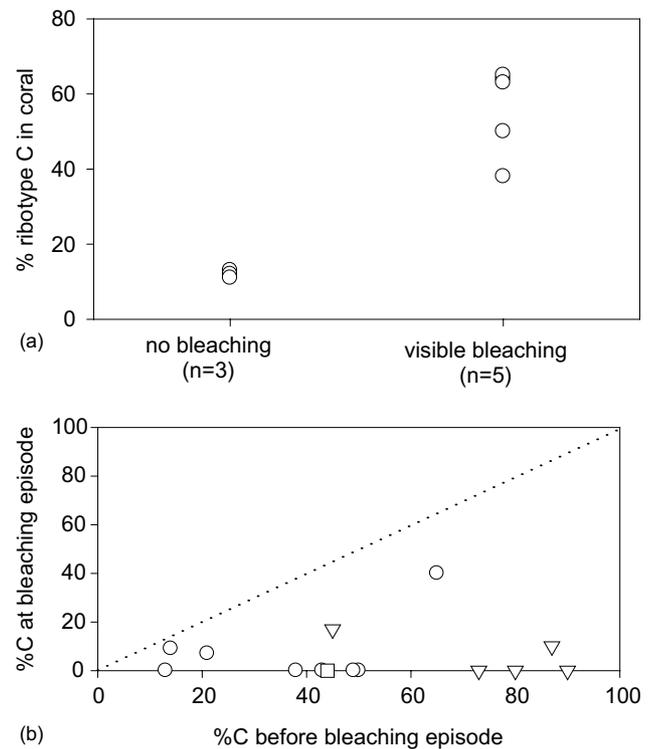

Fig. 3. Variation in bleaching susceptibility among ribotypes of *Symbiodinium* in corals of the *Montastraea annularis* species complex. (a) Ribotype C content of bleaching-resistant and bleaching-susceptible coral colonies containing a mixture of ribotypes B and C. (b) Impact of bleaching on ribotype C content of colonies containing a mixture of A + B + C (squares), B + C (circles) and A + C (triangles). [Redrawn from data in Fig. 4 of Rowan et al. (1997).]

4.2. Resistance to bleaching through acclimation

Insight into the processes underlying the bleaching susceptibility comes from the long-term study of Barbara Brown and colleagues on *Goniastrea aspera*, a member of a shallow water community of massive corals at Phuket, Thailand (Brown et al., 1996). The sea water levels in the region are low in the first months of the year, such that corals at the study site are fully emmersed at low tide (which happens to occur in the afternoon) for some days. If cloud cover is low, as is common place at this time of year, the west face of the exposed corals experiences high light levels, causing localised solar bleaching from which the corals recover promptly. In several years in the last decade, the sea water temperature in the region has exceeded the norm in April/May. This has caused thermal bleaching of the corals, apart from the west face recently recovered from solar bleaching (Brown et al., 2000).

The resistance of the symbiosis on the west face of the colonies cannot be attributed to within-colony genetic variation in *Symbiodinium* comparable to that observed by Rowan et al. (1997) for *Montastreaea* species (see Section 4.1), because the *G. aspera* colonies harbour an

apparently uniform *Symbiodinium* population of ribotype D (Brown et al., 2002a). Furthermore, the algal cells from the east and west faces of the corals did not differ significantly in levels of stress proteins, antioxidant enzymes or photoprotective xanthophylls, all of which would be predicted to contribute to protection against temperature/light-induced cellular damage. The animal tissues from the east and west faces of the corals, however, were biochemically distinctive: with significantly elevated levels the antioxidant enzyme superoxide dismutase and the stress proteins hsp60 and hsp70 on the west face, relative to the east face (Brown et al., 2002b). The implication is that the coral tissues acquire a tolerance of the conditions that promote bleaching through acclimatory biochemical changes in the animal partner.

4.3. Some wider implications

Two predictions arise directly from recent research on the variation in susceptibility to bleaching. First, *Symbiodinium* ribotypes A and D are anticipated to be favoured over ribotype C and possibly B in some animal species subjected to bleaching episodes. This may result in a shift in the dominant *Symbiodinium* ribotype to A/D in some species, and increased abundance of species capable of forming a symbiosis with these ribotypes. The impact on the species composition of host communities depends critically on the specificity of the symbioses, i.e. the taxonomic range of *Symbiodinium* with which they can associate. Various surveys using small samples sizes at one or a few sites have suggested that many host species are specific to single ribotypes or even subgroups of one ribotype [reviewed in Rowan (1998)], but more extended sampling protocols have identified two or multiple *Symbiodinium* ribotypes in various host species. Commonly, most host individuals bear one detectable ribotype, and a different ribotype is dominant in a low proportion of animals tested or at particular sites (e.g. Van Oppen et al., 2001; Toller et al., 2001b; Savage et al., 2002). The contribution of genetic, developmental and environmental factors to this variation is not known, but the data available suggest that many symbioses may be described more aptly as 'selective' than as 'specific' in their choice of algal partner. A complicating factor in these considerations is that the abundance of a symbiosis bearing a particular *Symbiodinium* ribotype is also predicted to be influenced by the impact of the acquired *Symbiodinium* cells on the performance of the host, including the long-term effects on growth, reproduction and resistance to disease. The physiological functions of *Symbiodinium* cells in symbioses recovered from bleaching and its impact on animal performance have not been investigated.

Second, symbioses that bleach in response to elevated temperature/irradiance and survive are anticipated to be more tolerant of subsequent episodes of elevated temperature/irradiance without a shift in the complement of *Symbiodinium* cells, as a result of physiological acclimation. Elements of the processes contributing to acclimation have been identified (Section 4.2), but their quantitative importance in the observed tolerance of bleaching triggers and the persistence of the acclimatory response over time remains to be established. The key issue is whether the response is sufficiently robust and persistent to support tolerance to projected climate change.

5. Why *Symbiodinium*-symbioses bleach

Animals and plants enter into symbioses with a wide diversity of micro-organisms, including micro-algae, and these associations are generally remarkably tolerant of variation in abiotic conditions (Douglas, 1994). Symbioses with *Symbiodinium* species are exceptional in that they commonly live in habitats at 1–2 °C below the temperature which triggers collapse of the symbiosis (i.e. bleaching) with negative consequences for the growth, reproduction and survival of the animal host (e.g. Szmant and Gassman, 1990; Meesters and Bak, 1993; Harvell et al., 1999; Wilkinson et al., 1999). In this respect, the symbiosis appears suboptimal. Symbioses are not fixed, and there are various instances over evolutionary time where the microbial partner in a symbiosis has been replaced by a phylogenetically distant partner, e.g. arbuscular mycorrhizal fungi by ectomycorrhizal fungi associated with roots of various trees (Brundrett, 2002), the bacteria *Buchnera* by yeasts in certain aphids (Fukatsu and Ishikawa, 1996), peridinin-containing plastids by various endosymbiotic algae in some dinoflagellates (Saldarriaga et al., 2001).

Why does the apparently deleterious trait of bleaching persist in *Symbiodinium* symbioses? One answer to this question is the adaptive bleaching hypothesis of Buddemeier and Fautin (1993). It is proposed that bleaching is an ecologically risky but adaptive strategy of the animal partner to replace an inferior symbiont by an alternative superior form. This stimulating hypothesis presupposes three processes.

(a) *The displaced symbiont is inferior to the invading symbiont*. As an example, Toller et al. (2001a) demonstrated that colonies of *Montastraea faveolata*, which bore ribotype C prior to bleaching, were occupied by ribotype A after recovery. Ribotype A can be described as more invasive than ribotype C, but invasiveness is not equivalent to superiority, which relates to the capacity to promote performance of the host. A useful parallel is provided by the nitrogen-fixing rhizobial bacteria in the root nodules of wild leguminous plants. Very commonly,

the populations of rhizobia in these plants fix nitrogen at low rates and promote relatively poor plant growth, but they are very competitive and infect the plant roots more efficiently than symbiotically superior strains (Thies et al., 1991; Denton et al., 2002). As considered in Section 4.3, the impacts of *Symbiodinium* ribotypes on host performance have yet to be investigated. For this expected process in the adaptive bleaching hypothesis, "the judge is still out".

(b) *Replacement of a resident* Symbiodinium *population in an animal requires depletion of the population.* Data from other symbioses provide support for this scenario. Specifically, hydra (a freshwater cnidarian) can be infected with strains of the green alga *Chlorella* that release much of their photosynthetically fixed carbon and support high growth rates of the hydra (superior strains) and strains that release little photosynthate and support low hydra growth rates (inferior strains). When symbioses between hydra and the inferior strains are incubated with a superior strain of *Chlorella*, the inferior strains are not replaced, even though the superior strains form an association readily with alga-free hydra (McAuley and Smith, 1982). The underlying mechanisms are obscure, but one possibility is that animal cells competent to house the symbiotic algal cells (a subpopulation of cells in the endodermal layer of Cnidaria) can acquire exogenous algal cells only if they lack a resident algal population, i.e. if they are 'empty host cells' and are not already infected with algal cells. These considerations suggest that this process of the adaptive bleaching hypothesis is plausible.

(c) *An alternative (putatively superior) strain of* Symbiodinium *is available to populate the bleached animal host.* In principle, the replacing *Symbiodinium* cells may be members of the residual population of algal cells in the bleached host or of external origin, i.e. in the water column. Residual populations are regularly observed in a bleached symbiosis, and they could repopulate the host relatively rapidly by proliferation within the few infected host cells, exocytosis from individual cells and subsequent uptake by 'empty host cells' within the same host (Jones and Yellowlees, 1997). The residual populations may include cells genetically different from the dominant *Symbiodinium* cells in the pre-bleaching association because some symbioses bear two-to-multiple *Symbiodinium* taxa, all but one at very low densities undetectable by the methods used routinely to type *Symbiodinium* populations (Santos et al., 2001). *Symbiodinium* cells have been detected in the free-living condition (Carlos et al., 1999). They are apparently not a common or abundant member of phytoplankton populations, but their incidence during bleaching events is unknown. To summarise,

plausible processes can be invoked to meet this prediction of the adaptive bleaching hypothesis, but the incidence (and relative importance) of alternative *Symbiodinium* cells in residual populations or external environment of bleaching symbioses remain to be quantified.

Among the several explorations of the adaptive bleaching hypothesis, the experimental approach of Baker (2001) is of particular note because it was conducted under field conditions. Colonies of several scleractinian coral species were reciprocally transplanted between deep (20–23 m) and shallow (2–3 m) locations on the Caribbean coast of Panama. The colonies transferred from shallow to deep suffered higher mortality than those transplanted in the opposite direction and only the latter displayed bleaching with replacement of *Symbiodinium* ribotype C. The correlation between coral survival and *Symbiodinium* replacement is consistent with the adaptive bleaching hypothesis, but the causal basis of the link is uncertain, i.e. there is no evidence that the superior survivorship of the deep-to-shallow transplants was a consequence of their bleaching.

These data indicate that the adaptive bleaching hypothesis and the three processes ('a' to 'c' above) on which it is founded remain unproven. It can be argued that the world's reefs are providing an unplanned experimental test of the adaptive bleaching hypothesis. The repeated demonstrations of depressed growth and reproduction, increased susceptibility to mechanical damage and disease, and, in some instances, mass mortality provide unambiguous refutation of the adaptive value of bleaching to symbioses under current environmental conditions.

In summary, it is obscure why bleaching occurs. In a historical sense, the adaptive explanation may be correct: that bleaching was of selective advantage to the animal hosts under different, and presumably more benign, environmental conditions than the present. Alternatively, bleaching may be a negative by-product of an otherwise advantageous or essential symbiotic trait (e.g. elimination of algal cells that are damaged or not releasing nutrients).

6. Conclusions

The experience of the last two decades suggests that bleaching is generally deleterious to corals and other *Symbiodinium* symbioses and to reef communities. Bleaching can, therefore, be considered as a linked group of ailments or diseases in the broadest sense of deleterious physiological responses (i.e. not restricted to pathogen-induced disease). It is probably unhelpful to describe bleaching as a single ailment, or to expect the

explanation of the causes of bleaching to be simple. As Section 3 and Fig. 1 illustrate, bleaching can be considered to comprise three elements (trigger, mechanism, symptoms), and some or all of the components of each element may not be uniform across different symbioses environmental circumstances.

The negative impact of bleaching is variable, from relatively mild in the seasonal bleaching observed on many reefs (see Section 2) to the mass mortality of all established corals on a reef. The suggestion that bleaching is adaptive is of considerable academic interest because it may explain why this trait has not been eliminated by selection (Section 5), but it is of limited apparent value in mitigating the negative effects on coral reefs of anthropogenic factors that promote bleaching.

Among the important studies on bleaching in recent years have been the demonstrations of genetic variation in the bleaching susceptibility of *Symbiodinium* and the acclimatory capabilities of the animal partner (Section 4). Furthermore, geographic variation in responses of the symbioses to temperature has been interpreted as indicative of variation in bleaching susceptibility of the animal partner (Hoegh-Guldberg, 1999). The quantitative impact on these factors in the projected incidence of bleaching can be explored by extension of current simulation modelling. Contrary to some claims (e.g. Risk, 1999), it is premature to "write-off" the *Symbiodinium* symbioses and the world's coral reef ecosystems as unable to tolerate the climate change. The need for sustained management of the reef ecosystems and protection from local anthropogenic factors is greater than ever.

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