



## Adaptive bleaching: a general phenomenon

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### Abstract

Laboratory and field data bearing on the adaptive bleaching hypothesis (ABH) are largely consistent with it; no data of which we are aware refute it. We generalize the ABH in light of these data and observations. The population of zooxanthellae within an organism is dynamic, the diversity of zooxanthellae is both surprising and difficult to ascertain, and field experiments demonstrate both turn-over in zooxanthella types and habitat-holobiont correlations. Dynamic change in symbiont communities, and the idea of an equilibrium or optimal community that matches the environment at a particular place and time, are concepts that underlie or emerge from much of the recent literature. The mechanism we proposed to explain responses to acute bleaching appears to operate continuously, thereby enabling the host-symbiont holobiont to track even subtle environmental changes and respond promptly to them. These findings enhance the potential importance of the ABH in the outcomes of acute bleaching, which can (1) accelerate this process of holobiont change, and (2) change the set of possible trajectories for how symbiont communities might recover.

### Introduction

The adaptive bleaching hypothesis (ABH) may be concisely defined as the proposal that the loss of photosymbionts has the potential to allow some representatives of the host species to re-establish a symbiosis with a different dominant alga, resulting in a new holobiont (also referred to as ecospecies or host-symbiont unit) that is better suited to the altered environmental circumstances (Buddemeier & Fautin, 1993; Ware et al., 1996). Such a re-shuffling has the potential to enhance long-term survival of the hosts, helping to reconcile the long-recognized paradox that coral reefs seem sensitive to environmental perturbation in the short term, but robust over geological time (Buddemeier & Smith, 1999). The framework of reefs is formed by scleractinian corals (and some other morphologically similar cnidarians) that, with few exceptions,

are symbiotic with intracellular photosymbionts; the massive deposition of calcium carbonate by reef-forming corals is physiologically related, in ways that are still not fully understood, to possession of these symbionts (e.g. Al-Horani et al., 2003).

The hypothesized ABH mechanism rests on five fundamental assumptions: (1) multiple types of both zooxanthellae and host species commonly co-exist; (2) a diversity of photosymbionts can live with many (but not necessarily all) hosts, and *vice-versa*; (3) different host-symbiont combinations may differ physiologically in aspects (particularly stress responses) that affect survival of holobiont, host, and perhaps symbiont; (4) bleaching provides the opportunity for repopulation of a host with different dominant photosymbiont (allochthonous or autochthonous); and (5) stress-sensitive holobionts have competitive advantages in

the absence of stress, which implies a reversion to stress-prone combinations under non-stressful conditions (Buddemeier & Fautin, 1993; Ware et al., 1996).

Knowledge of the symbiosis between the dinoflagellates commonly referred to as zooxanthellae and their animal hosts has grown enormously during the past decade. The host-symbiont system is now recognized as more dynamic than was previously thought. As Diekmann et al. (2002, p. 230) concluded, although 'the complexity and flexibility of the coral-zooxanthellae symbiosis is only beginning to be understood,' it is clear both that these 'symbioses are not evolutionarily constrained, species-specific associations ... [and] that symbioses are not random.' According to LaJeunesse et al. (2003, p. 2047), the ABH 'assumes that symbiotic associations are highly flexible and adapt rapidly to environmental change.' We summarize the data that validate this perspective, reviewing them in terms of the five assumptions cited above, and generalize the ABH in light of these findings.

In the discussion that follows, as in the original formulation, we use 'adaptation' in the standard English (non-Darwinian) sense: '... modification of an organism or its parts in a way that makes it more fit for existence under the conditions of its environment...' (Merriam-Webster, 1997). Mechanistically, this may subsume any combination of what biologists define as acclimation, acclimatization, or adaptation. Although this usage has been the source of some confusion (see 'Challenges to the ABH' below) because it is at odds with the narrowly-defined, specialized use of the term in evolutionary biology, we consider communication with non-specialists to be of paramount importance.

As the pace of environmental change accelerates, the frequency of bleaching is rising. Enough of these natural experiments, in addition to some manipulative ones, have been conducted during the past decade to reject the simplest falsification of the ABH – the null hypothesis that there is no difference in symbiont composition of a host individual or colony before and after an episode of bleaching (e.g. Baker, 2001; Glynn et al., 2001; Toller et al., 2001a). More specific considerations are presented in the following sections.

## Tests, validations, and uncertainties

### *Assumptions 1 and 2: diversity of hosts, photosymbionts, and holobiont combinations*

*Host diversity:* The diversity of photosymbiont hosts has long been recognized. In addition to the nearly 800 species of reef-building scleractinian corals (Veron, 2000), zooxanthellae form symbiotic relationships with many taxa of anemones, octocorals, hydrozoans, foraminiferans, molluscs, and sponges. Although the diversity of hosts is well established, identification of symbiotic combinations is complicated by problems with identifying hosts (e.g. Santos et al., 2001) and misapplication of host names (e.g. *Parasicyonis* sp. of Rodriguez-Lanetty et al. (2002) is *Entacmaea quadricolor*, and *Rhodactis* (*Heteractis*) *lucida* of LaJeunesse (2002) is *Ragactis lucida*).

*Photosymbiont diversity:* When the ABH was initially formulated, the diversity of zooxanthellae was thought by many to be small, although the early idea that all zooxanthellae belong to a single species, *Symbiodinium microadriaticum*, had been abandoned (e.g. Trench & Blank, 1987, and summaries by e.g. Buddemeier & Fautin, 1993; Kinzie et al., 2001; Santos et al., 2002). Three clades, the units commonly used in taxonomic surveys of zooxanthellae, were recognized at the time the ABH was published; at present, seven clades, containing ~60 distinguishable types, are recognized (e.g. Santos et al., 2002; Baker, 2003, 2004). LaJeunesse (2002, p. 395) estimated that '40 or more distinctive types populate invertebrate hosts in the Caribbean' alone. These clades and types are coarse estimates of the true diversity of these organisms (e.g. Santos et al., 2001, and references therein; Savage et al., 2002a; Goulet & Coffroth, 2003a, b). Recognition of this diversity and accurate identification of individual taxa are critical if stability or change in associations is to be reliably assessed.

*Holobiont (symbiosis) diversity:* Coexistence of multiple types of zooxanthellae in a single host had not been convincingly demonstrated at the time the ABH was proposed, but was inferred by analogy with coexisting zooxanthellae and zoochlorellae in some sea anemones (e.g. Secord & Augustine, 2000) – a situation known in other symbiont systems as well (Anderson et al., 1998).

It is now well established that colonies of a single species of coral may contain multiple types of symbionts (Rowan et al., 1997; Santos et al., 2001, 2003), commonly one abundant and one or more others as a few individuals or in low densities (summarized by Douglas, 2003). LaJeunesse (2002) found a few symbiont types that occur in many taxa of hosts, but rare types that have high host specificity. On the basis of literature reviews and study of *Madracis* on Curaçao, Diekmann et al. (2002, p. 226) considered 'one zooxanthellae type is probably the norm.'

As it has become possible to detect finer distinctions among photosymbionts and smaller populations of them, more diversity has been recognized even in corals that had been considered specialists (e.g., Darius et al., 2000; Toller et al., 2001b). Diverse photosymbionts have been identified in cultures derived from a single host, but these may comprise only a subset of those living in the source animal in nature, in part due to the low probability of sampling types present in small proportions, in part because some types are differentially favored through selection imposed by culture conditions (Rowan, 1998; Santos et al., 2001).

*Specificity:* Specificity such as found by LaJeunesse (2002) is not inconsistent with the ABH, which postulates variability in host-symbiont specificity across the range of both potential partners such that some hosts and photosymbionts may establish symbioses with only one, or a very few, taxa.

Among taxa capable of multiple partnerships, the ABH postulates various behaviors: only some zooxanthella types may be taken up by a given host (perhaps due to recognition mechanisms between partners: e.g. Diekmann et al., 2002; Baker, 2003), only some newly-acquired zooxanthella types may survive, and, among them, fewer may persist or dominate the ultimate holobiont. Symbiont specificity through time on the scale of 10 years was convincingly shown in the field by Goulet & Coffroth (2003a, b) for the octocoral *Plexaura kuna*, but this specificity is a feature of one stage in the organism's life history. The primary polyp of a colony of *P. kuna* acquires its zooxanthellae from the environment and can take up those of more than one clade (Coffroth et al., 2001), but only those of clade B persist. Once

established, the specific type of clade B zooxanthella associated with a genetically distinct host colony persisted through reciprocal transplants to different environments. Rodriguez-Lanetty et al. (2003) also showed stability in symbiont type at the clade level in sea anemones through time and space, but clade-level analysis does not reflect the functional diversity of possible photosymbionts.

Davy et al. (1997) followed the fate of allochthonous and autochthonous zooxanthellae through time in the sea anemone *Cereus pedunculatus*. Although zooxanthellae from the anemone *Anthopleura ballii* were taken up less readily than were those from other species, and autochthonous zooxanthellae were more persistent than allochthonous ones in the short term, in the longer term (36 weeks), densities of zooxanthellae from these two anemones were indistinguishable. Davy et al. (1997, p. 214) wrote 'The ability to establish symbioses with zooxanthellae from a range of sources may enable *C. pedunculatus* to adapt to different environmental regimes ... Alternatively, it may simply increase the anemone's chances of survival should it lose all of its zooxanthellae and have to acquire new symbionts.' These are not mutually exclusive; together, they encapsulate the ABH.

#### *Assumption 3: different host-symbiont combinations differ physiologically*

Differences have long been recognized in environmental tolerances and preferences of the host taxa (e.g. Veron, 1995, 2000) and the algal symbionts, *in vivo* and *in vitro* (e.g. Ciereszko, 1991; Kinzie et al., 2001; Savage et al., 2002b). However, the relevant unit of analysis is the holobiont (e.g. Rowan, 1998). As Buddemeier & Fautin (1993) and Ware et al. (1996) stated, the 'eco-species' is likely to have emergent properties not expected from knowledge of the partners in isolation (the additive model of their interaction by Ware et al. (1996) was a mathematical expedient). Toller et al. (2001b, p. 348) observed that for the animal partner, 'corals identified as members of the same species may not in fact be equivalent at the whole organism (holobiont) level,' and Rodriguez-Lanetty et al. (2001) demonstrated that one species of coral differs in photosymbionts with latitude.

Although different zooxanthella phylotypes differ physiologically, at least some photosynthetic traits do not correlate directly with characteristics of the phylotype (Savage et al., 2002b). Empirical observations of more than one zooxanthella type per colony, with different types predominating in different macrohabitats and microhabitats (e.g., Rowan et al., 1997), also make it clear that holobionts differ physiologically.

If holobiont physiology is an emergent property, rather than being additive or controlled by one of the partners, the long-running debate on which partner is responsible for observed tolerances (e.g. Edmunds, 1994; Diekmann et al., 2002; Bhagooli & Hidaka, 2003) is largely immaterial to the resulting pattern, however interesting and important it may be otherwise. Moreover, as stated by Burnett (2002, p. 105), although 'Ecophysiological plasticity of individual algal strains is limited ... multiple strains may provide a degree of flexibility to host:symbiont associations.'

*Assumption 4: bleaching provides opportunity for change of the dominant photosymbiont*

Advances in understanding relevant to the ABH are not limited to those involving the identity of symbiotic partners or their interactions. Recognition of the variety, ubiquity, and range of intensities of bleaching processes points to the conclusion that catastrophic bleaching may merely represent the extreme end of a continuum that includes natural fluctuations in symbiont standing stocks over seasonal timescales, and catastrophic (or even visually detectable) bleaching may not be required for adaptive or acclimatory responses in ecospecies (Fitt et al., 2000, 2001).

The symbiont flora of an individual coral colony can undergo quantitative change (change in relative proportions of pre-existing algal taxa) and apparent qualitative change (appearance or dominance of a taxon not previously detected – e.g., Rowan et al., 1997; Baker, 2001; Toller et al., 2001b); the various combinations differ physiologically (e.g. Fitt & Warner, 1995; Warner et al., 1999; Toller, 2001b). Although there has not yet been unequivocal demonstration of qualitative change by allochthonous uptake as a prompt response to natural bleaching, uptake and persistence of allochthonous zooxanthellae have been

demonstrated in field and laboratory experiments (Davy et al., 1997; Kinzie et al., 2001).

Hill & Wilcox (1998) and Toller et al. (2001a) found that severe bleaching allows establishment of novel associations, even if environmental conditions return to what they had been before bleaching. Moreover, zooxanthellae 'show patterns of dominance or prevalence similar to communities of free-living organisms' (LaJeunesse, 2002, p. 394). Thus, bleaching of any sort may open space in potential hosts for a wide variety of symbionts that are sorted not only in terms of their interactions with host and environment, but also among themselves (Baker, 2003, and references therein).

Changes in the dominant photosymbiont, whether from uptake of new partners following bleaching or from change in dominance of pre-existing internal populations, stem from stochastic processes, so the resultant holobionts may not be the same every time. Such change requires not only the ability to form diverse partnerships, but also, ultimately, the ability to acquire new (or multiple) symbionts from the environment, and the availability of such symbionts for acquisition.

Since some cnidarians do not acquire their symbionts maternally (= vertically) (e.g., Goulet & Coffroth, 2003b), infective zooxanthellae must generally be present in nature; Kinzie et al. (2001) demonstrated this and that uptake by bleached hosts is dose-dependent. Ralph et al. (2001) found zooxanthellae released from a coral host during bleaching to be physiologically functional; although not critical to assessing the ABH, this does mean that the population of possible partners is greater than if such cells were not viable.

Maternal transmission (see e.g., Benayahu & Schleyer, 1998, and references therein) of zooxanthellae is not necessarily identical with closed systems or highly specific symbioses. Diekmann et al. (2002) found no correlation of zooxanthella type with morphospecies of *Madracis*, in which zooxanthellae are transmitted maternally. Early embryos of the scyphozoan *Linuche unguiculata* acquire zooxanthellae maternally but later can acquire them from the environment – a system Montgomery & Kremer (1995) referred to as 'semi-closed.' Although the algae used in the experiments by Montgomery & Kremer (1995) were all autochthonous, the results indicate that maternal

acquisition may not preclude acquisition from the environment as well. Thus, in this respect also, the system may be more flexible than had been thought; rather than the vertical and horizontal (or closed and open) transmission alternatives that Rowan (1998, p. 412) thought might imply two 'evolutionary scenarios, probably with different consequences for symbionts diversification,' the two may be the end members of a continuum.

*Assumption 5: stress-sensitive holobionts have competitive advantages in the absence of stress*

Recent data are consistent with the model of the ABH by Ware et al. (1996) postulating that successive bleaching events eliminate types of photosymbionts sensitive to a particular stress, while types more resistant to the stress remain: Glynn et al. (2001) showed that zooxanthellae of Clade D have spread in the eastern Pacific recently at the expense of those of Clade C, and Toller et al. (2001b) inferred that zooxanthellae of clade D (see taxonomic assignments of Baker, 2003) dominate in certain circumstances not by dint of direct competition between algae, but because they tolerate conditions others do not.

In the experiments of Kinzie & Chee (1979) and Fitt (1985), autochthonous photosymbionts ultimately persisted whereas allochthonous ones did not. Reversion to the original combination is what might be expected under the ABH since the experiments were being conducted under conditions known to be favorable to the original holobiont – provided that there is some inherent preference for the stress-intolerant taxa, and/or that they contribute to superior holobiont fitness under low-stress conditions. This postulate of the model of Ware et al. (1996) is supported by general observations (only stress-resistant types should remain after repeated bleaching episodes without some countervailing advantage of the less resistant types), and by recent data of Van Oppen & Berkelmans (R. Berkelmans, personal communication). However, this is clearly one of the areas most urgently in need of additional research.

The issue of competitive advantage focuses on why the ABH is difficult to test by single experiments – it deals with population-level features, with responses that occur stochastically, and with the global environment over a long time, in all of

which rare events may be very important and in which correlative data are essential. These issues are dealt with more extensively by Buddemeier et al. (2004).

### Challenges to the ABH

Virtually all evidence adduced thus far is consistent with, much supportive of, and none fatal to, the ABH, contrary to the assertion of Hughes et al. (2003, p. 930) that 'A hypothesis that bleaching is 'adaptive,' increasing coral fitness by facilitating expulsion of susceptible zooxanthellae species and uptake of more resistant ones, has not been supported by observations on the fate of bleached corals.'

Some arguments purporting to falsify the ABH are based on single experiments or limited observations that are not robust tests of an hypothesis that operates stochastically and that deals with long times and broad patterns. For example, occurrence of an apparently single type of photosymbiont in a host organism or species, the same type of photosymbiont before and after bleaching, or the absence of a simple correlation between habitat and symbiont type, does not invalidate the ABH. In the case of highly specific symbioses, no change would be expected (or possible). However, for non-specific symbioses, the ABH posits a stochastic process, not a deterministic one, so bleaching need not inevitably lead to a changed symbiont flora (Buddemeier et al., 2004), and the probability of change depends on the variety of photosymbionts in the environment or the host – the greater the variety, all other things being equal, the more likely change will occur.

A practical issue affecting the validity of some purported tests is the coarseness with which diversity within the currently recognized clades can be resolved. Failure to observe replacement of one member of a clade by another may reflect absence of change or simply the inability of the analytical techniques used to detect the change that occurred; the same is true for detection of multiple symbionts. For example, Kinzie et al. (2001) observed that various subpopulations of zooxanthellae that were indistinguishable by the methods used in that study had very different physiological responses to changes in temperature, but Santos et al. (2002),

applying different molecular techniques to the same samples, found that unique responses corresponded to unique genetic sequences.

Misunderstanding or misstatement of the ABH has been persistent. Hoegh-Guldberg (1999) confined his critique of the ABH to heat stress, and Hoegh-Guldberg et al. (2002, p. 602) stated 'We consider that the evidence in favour of the ABH remains scant in the absence of observations that the genotypes of symbionts in corals become more thermally robust during and after mass bleaching' and 'we cannot conclude that bleaching favours new host-symbiont combinations that guard populations of corals against rising sea temperature.' Bleaching need not be 'mass' in nature, and the ABH is not restricted to heat stress. Ware et al. (1996, p. 201) used temperature as 'a convenient mathematical representation of a synergistic stress'; in fact, Fitt et al. (2001) posited synergism as well as dose-dependence among stresses. Further, Hoegh-Guldberg et al. (2002, p. 602) criticized a study by Baker (2001) by asserting that Baker 'is unable to distinguish newly invading genotypes from other rare genotypes that are already present in the host and which simply increase in proportion after conditions change.' As Baker (2002) pointed out in his rejoinder, this is irrelevant as far as the ABH is concerned.

The statement by Reaser et al. (2000, p. 1503) '... perhaps [corals] and their zooxanthellae may become more stress-tolerant (Buddemeier & Fautin, 1993; Ware et al., 1996)' implies they have misinterpreted the ABH as positing the evolution of stress-tolerance in the individual partners, as opposed to formation of more tolerant holobionts from individual partners that evolve new characteristics slowly.

The ABH has also been misstated in teleological terms. Hill & Wilcox (1998), for example, wrote 'corals bleach as the environment changes *in order to* acquire a new algal complement which is better adapted to current conditions' (p. 281, italics ours) and 'host invertebrates will expel and replace their resident algae with a symbiont more adapted to current environmental conditions' (p. 287). Variant teleological misstatements include 'there is no evidence that corals bleach specifically to exchange one genotype of zooxanthellae in their tissues for another' (Hoegh-Guldberg, 1999,

p. 856) and 'The ABH assumes that bleached corals favour new host-symbiont associations that optimize survival' (Hoegh-Guldberg et al., 2002, p. 602). The ABH *does not* state that a coral (or any animal host) *chooses* its symbionts; it *does* state that bleaching provides an opportunity for new combinations to arise, among which selection may occur for well-adapted ones (i.e., those that optimize survival), but does not *require* the combination to change.

In fact, although Hill & Wilcox (1998) interpreted their results as not supporting the ABH, the results are entirely consistent with it. They argued the pre-existing type of zooxanthella should have reinfected the sponge after bleaching since it represents the best-suited combination, but that a new type did. Alternative interpretations of their results are not mutually exclusive: one interpretation is that the new combination was due to the types of zooxanthellae available in the environment, another is that the new combination was actually superior.

Another source of debate about the ABH centers on the definitions of adaptation *vis à vis* acclimation and acclimatization (see Gates & Edmunds, 1999). The phenomenon, one aspect of which is loosely described as 'bleaching,' is an adaptation that we propose has allowed scleractinians to switch partners which, in turn, has allowed them to survive the large climate shifts through which they have persisted. As Baker (2002, p. 602) stated, 'if more rapid symbiont change proves beneficial, then bleaching has adaptive value.'

If the host-symbiont combination is regarded as a physiological unit, substituting a different zooxanthella type or changing the proportion of types alters the attributes of that unit. This is not acclimation in the usual biological sense since the genetic make-up of the unit has been altered, but contrary to the specialized biological use of the term adaptation, this does not require evolutionary time – it can be essentially instantaneous. Misinterpreting our use of the term 'adaptive,' Hoegh-Guldberg et al. (2002, p. 602) asserted 'The ABH ... necessitat[es] rapid evolutionary adaptation (that is, genetic change) by populations of reef-building corals and their symbionts.' The semantics of this debate are discussed by Baker (2004) and Buddemeier et al. (2004).

## Discussion and conclusions

We interpret recent evidence as supportive of our perspective that the animal-zooxanthellae relationship can respond dynamically to the environment, both biotic and abiotic. By analogy, lichens, a similar system consisting of algal and fungal partners, is not the tightly co-evolved symbiosis it had been considered (e.g., Piercey-Normore & DePriest, 2001). In fact, we conclude that our initial emphasis on adaptive response to obvious bleaching is too restrictive. The mass bleachings that appear to be increasing in severity and frequency are the results at one end of a continuum of environmental change over space and time. The zooxanthella density of an animal host varies through the year (Fagoonee et al., 1999; Fitt et al., 2000, 2001), blurring the definition of bleaching and contradicting the dogma that the population of zooxanthellae is kept within narrow limits by the host (e.g., Falkowski et al., 1993). Therefore, there seems to be a virtually continual opportunity for creation of new holobionts upon which selection can act and thus provide prompt, dynamic response of the symbioses to changing environmental conditions. In a neutral population genetic model for the cnidarian-algal symbiosis that she developed, Orive (submitted for publication) calculated that about one algal cell taken up from the environment every 50 days is sufficient to balance loss of genetic diversity due to drift, bottle-neck effects, etc. and thereby maintain within-organism zooxanthella diversity at its local maximum.

The existence and operation of the mechanisms proposed as part of the original ABH have been confirmed in many cases, and conclusively refuted in none. It now appears that adaptive change in the dominant symbiont can occur over the entire range from normal background fluctuations in algal populations to acute bleaching events. In the latter, the stress may (1) accelerate the process of change, and/or (2) change the set of possible trajectories for how these communities might recover by dramatically changing the starting abundance of each symbiont type and thereby shifting the system out of a region of local stability (where symbiont community structure tends to return to the same equilibrium after minor disturbance) into a region of relative instability (where many more recovery outcomes are possible).

Although further research is needed to clarify the environmental and evolutionary importance, detailed mechanisms, and extent of the ABH, we cannot improve on the statement by Baker (2002, p. 602): ‘The real question is not whether coral-algal associations can adapt by recombining, but rather how, and over what timescales, they do so.’

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