Reef corals bleach to resist stress

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ABSTRACT

A rationale is presented here for a primary role of bleaching in regulation of the coral–zooxanthellae symbiosis under conditions of stress. Corals and zooxanthellae have fundamentally different metabolic rates, requiring active homeostasis to limit zooxanthellae production and manage translocated products to maintain the symbiosis. The control processes for homeostasis are compromised by environmental stress, resulting in metabolic imbalance between the symbionts. For the coral–zooxanthella symbiosis the most direct way to minimize metabolic imbalance under stress is to reduce photosynthetic production by zooxanthellae. Two mechanisms have been demonstrated that do this: reduction of the chlorophyll concentration in individual zooxanthellae and reduction of the relative biomass of zooxanthellae. Both mechanisms result in visual whitening of the coral, termed bleaching. Arguments are presented here that bleaching provides the final control to minimize physiological damage from stress as an adversity response to metabolic imbalance. As such, bleaching meets the requirements of a stress response syndrome/general adaptive mechanism that is sensitive to internal states rather than external parameters. Variation in bleaching responses among holobionts reflects genotypic and phenotypic differentiation, allowing evolutionary change by natural selection. Thus, reef corals bleach to resist stress, and thereby have some capacity to adapt to and survive change. The extreme thermal anomalies causing mass coral bleaching worldwide lie outside the reaction norms for most coral–zooxanthellae holobionts, revealing the limitations of bleaching as a control mechanism.

1. Introduction

Bleaching of scleractinian corals has been documented with and without mortality of corals in response to a variety of environmental parameters and under conditions of stress (Glynn, 1993; Brown, 1997a; Coles and Brown, 2003). In the last two decades, mass bleaching events associated with widespread mortality of corals following anomalously high seawater temperatures (Glynn, 1993; Brown, 1997b; Hoegh-Guldberg, 1999; Hughes et al., 2003) have raised bleaching to the forefront of research and public awareness on coral reefs. Because of the dramatic association of bleaching with mortality, bleaching has earned the label of being a pathology (Douglas, 2003, Rosenberg and Falkovitz, 2004) and an external disturbance (Hoegh-Guldberg, 1999; McClanahan et al., 2002; Bellwood et al., 2004).

The role of bleaching in scleractinian corals is complex and has been covered by a number of reviews and syntheses that cross a broad spectrum from environmental triggers to physiological and ecological responses (Glynn, 1993; Brown, 1997b; Hoegh-Guldberg, 1999; Ostrander et al., 2000; Coles and Brown, 2003; Douglas, 2003; Fautin and Buddemeier, 2004; Hoegh-Guldberg et al., 2004; Obura, 2005). It is not my aim to comprehensively review the literature nor query specific statements of authors. The motivation for this paper comes from a continuing gap in our understanding of the relevance and role of bleaching for the evolutionarily relevant unit – the holobiont, and its constituent symbionts. Reductionist research on individual metabolic and stress pathways is necessary to delineate and describe specific mechanisms of bleaching (Buddemeier and Fautin (1993)); however, these are not sufficient for understanding the holobiont level phenomenon that is integrated over several of these pathways. At this higher level, contrary statements are made in the literature that bleaching may be pathological (e.g. Douglas, 2003) or adaptive (Baker, 2001), or even both... “Buddemeier and Fautin (1993) proposed that bleaching is not merely pathological, but is also adaptive...” (Ware et al., 1996, p. 200). Bleaching has been presented as regulation, stress and adaptation, but without an organizing principle that reconciles the contradictions among these concepts.

1.1. Bleaching and regulation

Early laboratory work on the coral–zooxanthella symbiosis explored aspects of regulation of relative biomass, energy exchange and nutrient metabolism of the symbionts. Key processes...
examined included carbon and energy budgets between symbionts (Muscatine et al., 1972; Muscatine, 1990), stable zooxanthellae to coral biomass ratios (Muscatine et al., 1998), zooxanthellae expulsion (Baghdasarian and Muscatine, 2000), and nitrogen availability and metabolism (Wilkinson and Trench, 1986; Falkowski et al., 1993; Szmacint and Gassman, 1990), among others (e.g. see Smith and Muscatine (1999)). Field studies found natural variation in zooxanthellae densities that tracked annual cycles in environmental parameters such as temperature, light and nutrient availability (Stimson, 1997; Brown et al., 1999b; Fagoonee et al., 1999; Fitt et al., 2000). Lowest levels of zooxanthellae density during these normal annual cycles were associated with paling of the coral tissue surface, and even bleaching.

1.2. Bleaching and stress

Corals bleach under a broad range of external stimuli (triggers, sensu Douglas, 2003) when these exceed normal levels and become stressful (Brown, 1997a), for example at the extremes of annual ranges mentioned above. Stimuli that elicit bleaching include high and low temperatures (Porter et al., 1989; Gates, 1990; Glynn and D'Croz, 1990), high and low light levels (Coles and Jokiel, 1977), low salinity (Goreau, 1964), sedimentation (Rogers, 1990), xenobiotics (Brown, 2000) and general stress (Brown, 1997a). Under stressful conditions, mechanisms of bleaching include reduction in the pigment content of zooxanthellae (reduction in chlorophyll a and c2) and in the density of zooxanthellae in coral tissues (Brown, 1997b). Reduction in chlorophyll concentration within zooxanthellae may occur by a variety of mechanisms, for example damage to photosystem reaction centers (Warner et al., 1999) and disruption of dark reactions (Jones et al., 1998). Reduction in zooxanthellae density may occur by a number of mechanisms with varying levels of damage to the host cells that increases at higher stress levels (Glynn et al., 1985; Gates et al., 1992; Brown et al., 1995; Lesser and Farrell, 2004): cellular digestion of zooxanthellae, exocytosis of zooxanthellae, programmed cell death (apoptosis), normal cell death (necrosis) and host cell detachment.

Bleaching is not the first response to an external stress; it can be avoided if other responses specific to a stressor pre-empt physiological stress. For example, stimulation by high temperature and radiation may elicit some or a combination of the following responses before bleaching is induced: photoinhibition and photoprotective responses (Brown et al., 1999a), nonphotochemical quenching (NPQ) that dissipates excess light as heat (Warner et al., 1996; Brown et al., 1999b), increased production of fluorescent pigments that may act as sun-block (Salih et al., 2000), increased production of heat shock proteins that repair heat-related damage to other proteins (Downs et al., 2000), oxidative enzymes that sequester oxygen radicals (Downs et al., 2002) and adaptive responses of host and symbiont (Coles and Brown, 2003). Depending on the capacity of these mechanisms to keep internal physiological stress below a threshold for bleaching, bleaching may be initiated at intermediate levels of their expression, or once their maximum limits are exceeded.

1.3. Bleaching and adaptation

The adaptive bleaching hypothesis (ABH) was first expounded by Buddemeier and Fautin (1993) and further developed through a series of papers broadening its foundation in a number of areas including modeling of zooxanthellae population dynamics (Ware et al., 1996), evidence supporting symbiont changes following bleaching (Baker, 2001; Baker et al., 2004), evidence for physiological and phylogenetic diversity among zooxanthellae (Rowan, 2004; Rowan et al., 1997), relationships between bleaching and disease (Buddemeier et al., 2004) and clarifications of its scope and conceptual underpinnings (Fautin and Buddemeier, 2004). The ABH presents bleaching as a mechanism that enables the exchange of symbionts that results in a better fit of the holobiont to a changed environment. Its exposition is based on five key assumptions (Buddemeier and Fautin, 1993): (1) multiple taxa of both zooxanthellae and coral commonly co-occur, (2) some zooxanthella and host taxa may have multivalent associations with one another, (3) stress limits beyond which the symbiosis is disrupted are characteristic of the holobiont as opposed to one or other symbiont alone, (4) bleaching provides an opportunity for the host to be repopulated by different zooxanthellae taxa, and (5) stress-sensitive symbioses have a competitive advantage in the absence of stress. Proponents of the ABH claim increasing support for each of these assumptions (Ware et al., 1996; Fautin and Buddemeier, 2004) while opponents deny this support on the basis that evolutionary change has not been demonstrated (Hoegh-Guldberg et al., 2002; Hughes et al., 2003).

Debate for and against the ABH (e.g. see Hoegh-Guldberg (2005)) has been beset by two primary problems. First, the ABH has been criticized primarily by researchers applying a reductionist physiological approach, working on specific mechanisms of regulation and/or resistance to specific stressors. From this point of view the apparent pathological role of bleaching has appeared dominant, further research demonstrates an increasing diversity of mechanisms, responses and interactions, and the timescales and mechanisms sufficient to demonstrate evolutionary change are mismatched. Second, proponents of the ABH have shied away from stating a full Darwinian exposition of adaptive significance. The term adaptive is used only in its vernacular sense (Buddemeier et al., 2004) with the caveat "...in the discussion that follows, as in the original formulation, we use 'adaptation' in the standard English (non-Darwinian) sense..." (M)echanistically, this may subsume any combination of what biologists define as acclimation, acclimatization, or adaptation..." (Fautin and Buddemeier, 2004, p. 460). While this may ease communication it evades the primary need to develop an evolutionary hypothesis.

1.4. Metabolic innovation, energy and consequences for symbiotic homeostasis

One of the major consequences of symbiotic associations is the access to metabolic innovation for the host (Douglas, 1994). The main metabolic novelty for the coral host is the photosynthetic capacity of the endosymbiotic zooxanthellae, which has been demonstrated to affect a broad range of host functions including respiration, growth, calcification, mucus secretion, reproduction and regeneration (e.g. Muscatine, 1990; Douglas, 2003). Concern here is the most basic and direct metabolic interaction between host and symbiont, which is related to photosynthetic production by zooxanthellae and its fate in the holobiont (i.e. its translocation, use and management by the coral) and direct by-products and side effects of physiological mechanisms involved in these functions. The symbiosis pairs two organisms with fundamentally different rates of metabolism (Willkerson et al., 1988): a single-celled dinoflagellate with potential doubling times of two days, and an animal host limited by tissue growth and skeletal formation. From this perspective the primary problem for the symbiosis is managing (limiting) metabolism (photosynthetic production) of the symbiont. A stable symbiosis would require that one or both partners express regulatory mechanisms that can limit zooxanthellae production, raise the use of fixed carbon by the host, shed potential excess photosynthesate that the host cannot metabolize, and manage biomass relations between the two (Fig. 1; see Falkowski et al. (1993)). This is the converse problem to the main focus of research, which turned to maximization of utilization by the host, and demonstrating how the heterotrophic coral could function with its
symbiont as an autotroph in laboratory and field conditions (e.g. Muscatine et al., 1981; Edmunds and Davies, 1986, 1989).

1.5. Tradeoffs and life history strategies

Organisms have limited resources that must be allocated to maintenance, growth and reproduction (Stearns, 1992), requiring tradeoffs between them. Successful strategies of resource allocation can be described in a number of ways, of which the r and K life history strategies developed for terrestrial animals (MacArthur, 1960) have dominated theoretical and empirical studies. The tradeoffs that are the foundation of these opposing strategies are rapid growth and early reproduction (r), i.e. high rates of metabolism, versus slow growth and long generation times (K), i.e. slow rates of metabolism. Alternative models have been described that incorporate other traits such as phenotypic plasticity (Grime, 1977; Greenslade, 1983). Under adverse conditions (Fig. 2, panel a) regulation of the symbionts lies within normal limits (e.g. of seasonal changes in zooxanthellae and pigment density) without the expression of any stress responses. At increasing levels of the stressor (panel b) a broad range of first-order physiological stress responses, depending on the specific stimulus, may act to relieve stress. The induction and maximum thresholds and slope (counteractive capacity) of each of these stress responses will vary according to many factors. At a certain point however (transition from panel b to c), these individual responses become insufficient to maintain symbiotic balance.

At this point either the functional symbiosis would break down, or a second order stress response may be postulated that directly manages the fundamental biomass and/or energy relations of the symbiosis, as differentiated from the various first-order responses which address individual physiological mechanisms. As the induction threshold of this second order stress response is crossed its most simple action would be an adversity response that reduces the metabolic imbalance in the holobiont by down-regulating photosynthetic production. This could be achieved by three alternatives for control: (i) reducing the photosynthetic rate of individual zooxanthellae without altering their productive capacity, (ii) reducing the photosynthetic rate of individual zooxanthellae by degrading their productive capacity, or (iii) reducing the biomass ratio of zooxanthellae to coral. Reduction in pigment concentration in zooxanthellae and reduction in zooxanthellae density (options (ii) and (iii), respectively) have been documented in the literature (see Section 1) but as yet option (i) has not been reported.

Considering only reduction in the biomass of zooxanthellae for simplicity, expression of this response increases progressively with the increasing stressor (Fig. 2, panel c) until no further changes are beneficial, or the metabolic or other costs to the holobiont are too large to be easily reversed when normal conditions return, and the stages, stress resistance, competitive ability, and maximum colony size.

An explicit life history model is essential for relating individual traits, such as bleaching, to Darwinian fitness. To do this it is necessary to know how the trait is expressed over a full environmental gradient, i.e. its reaction norm, the subject of gene–environment interactions (Via and Lande, 1985; Stearns, 1992). High variability in coral bleaching responses has been amply documented at intra-colony and between-colony levels, across multiple scales of spatial and temporal variation, and across taxonomic divisions of both coral and zooxanthellae (Coles and Brown, 2003). This variation enables the construction of a reaction norm for the bleaching response that enables inferences to be made of genetic vs. environmental contributions to observed variation, and of selection pressures towards different life history outcomes.

2. The model

While bleaching has long been understood as a stress response (Brown, 1997a; Ostrander et al., 2000; Coles and Brown, 2003), the metabolic imbalance and life history arguments used here establish a novel premise for explaining its dynamics. This model is based on the stress response syndrome (SRS) or general adaptive mechanism (GAM) of Stebbing (1981, quoting Selye, 1946). An SRS deals with a system under homeostatic (or homeorhetic) control by regulatory systems that sense disturbances to states or rates in the system (Stebbing, 1981). Consider a coral–zooxanthella symbiosis as the model system, to which a simple external stress is applied (e.g. temperature, as in Ware et al. (1996)), that as it increases intensifies the imbalance between metabolic activity of the symbionts. The functionally intact symbiosis is a controlled state in which under benign conditions (Fig. 2, panel a) regulation of the symbionts lies within normal limits (e.g. of seasonal changes in zooxanthellae and pigment density) without the expression of any stress responses. At increasing levels of the stressor (panel b) a broad range of first-order physiological stress responses, depending on the specific stimulus, may act to relieve stress. The induction and maximum thresholds and slope (counteractive capacity) of each of these stress responses will vary according to many factors. At a certain point however (transition from panel b to c), these individual responses become insufficient to maintain symbiotic balance.
Counteractive capacity of the stress response is exceeded. Past this maximum, the symbiosis declines irreversibly, because damage to one or both symbionts associated with the maximum threshold is too high, or activity by remnant zooxanthellae exceeds other tolerance limits of the coral. Thus, following induction of this stress response the coral tissue becomes transparent due to expulsion of the zooxanthellae and the white skeleton becomes visible, giving rise to the term ‘coral bleaching’. However, damage to the symbiosis that makes repair and recovery less likely, and mortality more likely, only occurs near and beyond the maximum capacity of the bleaching response (Fig. 2, panel d).

3. Discussion

3.1. Bleaching, regulation and stress

The crux of relating observations on coral bleaching to this hypothesis that it has a primary role as a homeostatic control mechanism is in distinguishing between conditions in which bleaching can fulfill its function, defined by panel c in the model, and conditions in which its counteractive capacity is exceeded, defined by panel d (Fig. 2). Mild bleaching is often reported during seasonal high temperature maxima and during periodic stress events such as seasonal river plume events. These recurring episodes of environmental stress repeat within the lifetime of the holobiont, thus qualify bleaching to be considered like any other homeostatic mechanism. Under these conditions bleaching may play a regulatory function within the genetic capacity of the symbionts.

On the other hand, extreme environmental excursions (e.g. high temperature anomalies) may lie beyond information contained in the genes of corals and zooxanthellae. The bleaching response may be induced under these conditions but as a result of its inadequacy mortality of the symbionts may occur. This ‘extraordinary bleaching’ (Fig. 2, panel d) may be visually indistinguishable from ‘normal’ (regulatory) bleaching (panel c). In this model normal and extraordinary bleaching are zones along a reaction norm (panel c vs. its transition into d), and there may be a broad transition between them that may vary with many different internal and external factors. Much as pre-bleaching stress (and thereby evidence of pre-bleaching first-order stress responses, Fitt et al., 2000) can be shown using PAM fluorometry (Jones et al., 1999), the development and use of more sensitive physiological tools is likely to help distinguish normal from extraordinary bleaching, to more closely define the boundaries of the bleaching reaction norm. Species-specific bleaching thresholds, both of lower and upper limits of susceptibility, and their variation over space and time, and with acclimatization, have generally been viewed as a problem (reviewed in Coles and Brown (2003)). However, from the perspective of this hypothesis, these differences are a foundation of bleaching, the problem being to define their limits and action, not their existence.

This model provides a framework to explain why individual mechanisms cannot explain the ‘whole’ of bleaching (Fautin and Buddemeier, 2004). Different mechanisms may be induced individually or together in response to different or multiple triggers and/or levels of stress (Fig. 2, panel b), and are not mutually exclusive (Coles and Brown, 2003). This is the foundation of Douglas’ (2003, p. 390) statement that it is “...probably unhelpful to view bleaching as a single ailment...”. An SRS model requires that bleaching be understood in terms of the internal state of the symbiosis as a function of its responses to external stimuli, not as a direct function of the external stimuli. Thus, while a wide range of regulatory mechanisms are induced in response to different external stressors, the bleaching mechanism itself is induced in response to internal imbalance, in symbiotic metabolism, resulting from inadequate regulation by these first-order stress responses. The analogy of a funnel, where a broad spectrum of different initial responses lead to one last-resort response system is useful in reconciling the many different and often conflicting mechanisms and triggers of bleaching in the literature, including bacterial bleaching (Rosenberg and Falkovitz, 2004).
The symbiosis and its control systems must be put into context of what happens at and beyond the reaction norm of the symbiosis. Why have control systems that minimize damage? Why does the symbiosis not remain intact all the way up to the point of mortality? One answer is generic; that minimizing damage related to outer limits minimizes costs associated with the limits thus enhancing a return to normality if and when conditions improve. The second answer is specific to adversity responses (Greenslade, 1983), where the environmental envelopes that the symbionts can inhabit while separated or when full symbiotic function is suppressed may differ from that which they inhabit while fully functional (and see Fautin and Buddemeier (2004)). Thus, if it is possible for coral and zooxanthellae to survive separated in panel d (Fig. 2), then a control system that manages how they separate in a way that minimizes damage is beneficial. Finally, this may also have beneficial consequences by minimizing barriers to recombination after conditions become benign (return from panel d to c–a). Thus, within the normal regulatory range for bleaching, it would be expected that both symbionts would respond to selective pressures to reduce the costs of bleaching to minimize damage and enable greater survival and/or more rapid recovery.

3.2. Bleaching and adaptation

The recent recognition of the diversity of zooxanthellae taxa (clades) made possible by advances in molecular techniques (Lajeunesse, 2001) supports the innovations that the ABH first expressed in 1993 (Buddemeier and Fautin, 1993). Assumptions 1–3 of the ABH are now demonstrated as facts. There will be a great deal of debate in coming years on the degrees of freedom in these interactions (e.g. Goulet, 2006; Baker and Romanski, 2007; Mieog et al., 2007) but it is incontrovertible that genetic variability in host–symbiont combinations does influence bleaching responses, and as a result natural selection can act on the constituent symbionts affecting their contribution to future generations.

Understanding the selective pressures on the bleaching response (assumptions 4 and 5 of the ABH) has been problematic. Life history strategies described for corals (Bak and Engel, 1979; Kojis and Quinn, 1984; Cameron and Endean, 1985; Jackson and Hughes, 1985) are consistent with the primary life history trade-offs between investing in growth and/or reproduction vs. stress resistance (Macarthur, 1960; Greenslade, 1983; Stearns, 1989). However, differences between ‘winners and losers’ with respect to bleaching have been described more on the basis of gross morphology, such as colony shape and tissue thickness (e.g. Loya et al., 2001; McClanahan, 2004). The SRS model interprets bleaching responses on the basis of the metabolism of the symbiosis providing a mechanistic framework that aligns selection pressures for bleaching with those for growth vs. stress resistance (Fig. 1) (Obura, 2001, in review; Buddemeier and Fautin, 1993). Thus, corals that maximize growth or reproduction are predicted by this model to have a tendency to bleach at lower stress levels and suffer higher mortality after bleaching, while corals that invest in stress resistance are predicted to bleach at higher levels of environmental stress and suffer lower mortality after bleaching.

Assumption 4 of the ABH deals with the adaptive exchange of symbionts. Based on the model presented here, a range of acclimative and adaptive options are available to the symbionts (Table 1). Selection for traits that are controlled by only one of the host or symbiont genomes follows standard possibilities and constraints on passing successful traits to future generations (Table 1, left column). However, for some traits of the holobiont, a new dimension of intra-generational genetic change is possible (Table 1, right column), as the host and symbiont genomes are not irrevocably tied to one another. This model predicts that directional selective pressure can result in a shift to a more fit holobiont through symbiont exchange (where multivalent symbiont associations are possible, assumption 2 of the ABH). Thus, the following patterns in zooxanthellae population responses observed in the holobiont: fluctuating symbiont densities (Brown et al., 1999a,b; Fitt et al., 2000; Fagoo- nee et al., 1999), symbiont shuffling under normal seasonal fluctuation (Chen et al., 2005), symbiont shuffling under more extreme environmental stress (Berkelmans and van Oppen, 2006) and symbiont switching after bleaching due to severe stress (Baker, 2001; Baker et al., 2004) are simply graded expressions of the same general syndrome at different points along the environmental continuum (Fig. 2).

The metabolic innovation of the coral–zooxanthellae symbiosis – high production and growth – is also its Achilles heel, revealed by the necessity for a bleaching response. The symbionts have not evolved to the point of being able to coexist without the final recourse of breaking down the symbiosis under stress. It can be postulated that should control option (i) described in the model evolve (photosynthetic activity of zooxanthellae could be completely shut down without degrading their productive capacity), there would be no need for the symbiosis to have a bleaching mechanism, and the association could evolve to become fully obligate at the cellular level. The label stress response syndrome applies in straightforward fashion to the responses of the coral host to stress within the symbiosis, but the label general adaptive mechanism may be more appropriate to incorporate the population–level interactions (see Selye (1946) and Stebbing (1981)) between zooxanthellae and their host. If an SRS/GAM model for bleaching is correct, the term ‘adaptive bleaching’, that has been the foundation of the debate system such as the bleaching response has evolved under. Hence the high levels of observed mortality of corals in spite, not because, of bleaching. These extreme events reveal the limitations of the control mechanisms, not their non-existence. Importantly, they reveal the limits to the adaptive capacity of Table 1

| Acclimatization/ adaptation options for the coral–zooxanthellae holobiont that may occur under the predictions of the SRS/GAM bleaching model. Both coral and zooxanthellae are subject to normal selective pressures acting on their genomes in isolation. Their association in symbiosis offers an additional level of options for both acclimation and adaptation. Definitions are taken from Coles and Brown (2003): acclimation refers to phenotypic changes in an organism under artificial or experimental conditions (not used here), acclimatization refers to the same under natural conditions, and adaptation refers to selection at the inter-generational level through reproduction and transmission of surviving genes. |
|---|---|
| Single organism/genome | Symbiosis/two genomes |
| Acclimatization | Adaptation | |
| Experience-mediated shifting of the bleaching reaction norm (thresholds) along the environmental gradient (by the coral, zooxanthellae or both) Selective mortality, sexual recombination of alleles and recruitment producing higher frequencies of symbionts that can survive extant conditions (of the coral, zooxanthellae or both) | Symbiont shuffling/switching that alters the genetic makeup of the holobiont Selective recombination following sexual reproduction (coral larvae take up zooxanthellae from the water column that differ from those of the previous generation) |
bleaching. The degree of stress to which bleaching is adapted can- not be far outside the history of coral and/or zooxanthellae gen- omes or the plasticity of mechanisms underlying its reaction norm, limiting the degree of change that can be tolerated. That bleaching may not be pathological does not in any way negate the critical threat posed by climate change to coral reefs as revealed by mass bleaching and mortality events (Glynn, 1993; Hughes et al., 2003; Hoegh-Guldberg et al., 2008).

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