

Bleaching as a life history trait in coral-zooxanthellae holobionts – relevance to acclimatization and adaptation

D.O. Obura

CORDIO East Africa, P.O.BOX 10135, Mombasa 80101, Kenya. dobura@cordioea.org

Abstract. This paper explores the relationship between bleaching patterns and growth strategies of coral-zooxanthella holobionts in relation to tradeoffs in benign and stressful environments. Growth strategies can be differentiated between growth/production maximizing versus stress tolerating/persistent options. The former are dependent on high growth (or reproductive) rate for competitive success and extension over space; their tradeoff is a high opportunity cost of reducing production, i.e. of an adversity response when stressed. The latter are dependent on their ability to persist under adverse conditions to maintain control over space; their tradeoff is low performance under good conditions. Obura's (2009) model for stress resistance in corals predicts that bleaching is induced under stressful conditions to reduce excess production by zooxanthellae and thereby maintain symbiotic balance. This hypothesis is consistent with bleaching responses where corals that invest in rapid growth (/reproduction) tend to bleach and die at lower levels of stress (e.g. *Acropora*, *Pocillopora*), while corals that invest in stress resistance tend to bleach and survive at higher levels of environmental stress (e.g. *Porites*). These bleaching/life history strategy patterns shed light on the scope for acclimatization and adaptation of corals, independently of the multiplicity of mechanisms that are precursors to the bleaching response.

Keywords: bleaching, symbiosis, scleractinian coral, zooxanthellae, climate change, environmental stress

Introduction

Obura (2009) presents a model for coral bleaching that reconciles the adaptive role of bleaching (Fautin and Buddemeier 2004) with the many competing interpretations of bleaching in the literature (Hoegh-Guldberg 2005) (Fig. 1). The model is based on life history tradeoffs between fast growth and reproduction versus stress resistance and persistence (Grime 1977, Stearns 1989, Greenslade 1983) and interpretation of bleaching as a Stress Response Syndrome (SRS) or General Adaptive Mechanisms (Stebbing 1981).

The model is based on the premise that the life history strategies of the space-dominating (e.g. *Acropora*) and opportunistic strategies of small branching (e.g. pocilloporid) corals require high investment in maintaining high photosynthetic activity by zooxanthellae and consequently high metabolic activity of the holobiont to utilize and manage this energy. Conversely, the stress tolerant strategies characterized by large long-lived massive (e.g. *Porites*) and many small slow-growing (e.g. *Siderastrea*) corals require commitment to an adversity response to stress, i.e., the ability to survive at low metabolic levels during stress to

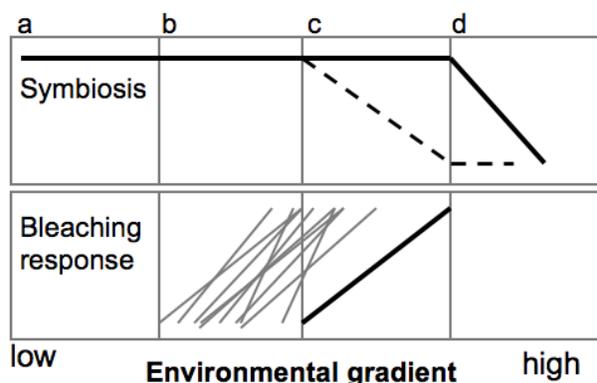


Figure 1. Stress Response Syndrome (SRS) or General Adaptive Mechanism (GAM) model (Stebbing 1981) for coral bleaching (Obura 2009). The intact symbiosis is maintained in balance (panels a-c, top) by homeostatic control mechanisms, but declines to zero (mortality, panel d) when the control mechanisms are exhausted. At low levels of stress a variety of first order stress responses (e.g. photo-chemical quenching, induction of heat shock proteins) sensitive to environmental stimuli (grey lines, panel b, bottom) may be induced, depending on the external stress. Once their tolerance range (counteractive capacity) is exceeded a second order control system sensitive to internal stress, the bleaching response, is activated (panel c, bottom), during which coral colour decreases (dotted line, top panel), but the symbiosis is intact and health (solid line, panel c, top). Once the maximum threshold for bleaching is exceeded, homeostasis is impaired, and the holobiont begins to break down irreversibly (panel d). Adapted from Obura (2009).

Table 1. Life history strategies based on the primary literature on animals and plants, and observational/empirical strategies described for stony corals.

<i>Equilibrium/Competitive</i>	<i>Opportunistic/Ruderal</i>	<i>Persistence/Adversity</i>	<i>Source(s)</i>
Primary models			
Density dependence, low rates of increase, thrive in predictable conditions.	Density independence, high rates of increase, thrive in unpredictable conditions.	Adaptation to predictably unfavourable environments. Slow rates of increase, low abundance, persistence.	MacArthur 1960, Pianka 1970, Greenslade 1983
Highly competitive, large size, fast growth.	Opportunistic, small size, fast growth, ephemeral.	Stress-tolerant, varied growth forms, slow growth, long lifespan.	Grime 1977
Empirical coral models			
N/a	Opportunistic, fast growth rates, high sexual and/or asexual reproduction, monopolize space in short term. High turnover. <i>Acropora, Pocillopora.</i>	Adaptations to low abundances, persistence through varied environmental conditions. <i>Porites.</i>	Cameron and Edean 1990
Branching, high reproductive output (spawners), low recruitment, high survivorship of juveniles, high fragmentation, high regeneration fast growth rates, long-lived but with senescence. <i>Acropora.</i>	Foliaceous/branching, high recruitment, fast growth, high tissue turnover, high partial and full mortality, small adult size, low competitive abilities, low regenerative abilities. Small agariciids, pocilloporids.	Massive, low recruitment, high survivorship, slow growth, low partial mortalit, fragmentation important, long life expectancy, low tissue turnover, large adult size, competitively aggressive, resistant to sediment, high regeneration. <i>Montastrea annularis, Porites</i>	Bak and Engel 1979, Jackson and Hughes 1985, Kojis and Quinn 1994

endure it until conditions improve (Greenslade 1983, Hoffman and Parsons 1991). These expectations are consistent with predictions of life history theory (Stearns 1992), which distinguishes between strategies that maximize or invest in growth and/or reproduction (production) vs. those that maximize survival through stress resistance (persistence). These strategies impose opposite constraints on many organismal processes, and require investments from a limited resource base (Stearns 1989). In the terms of the two main strategy concepts explored in the plant and animal literature – the r-K theory of MacArthur (1960), and the CSR theory of Grime (1977), these can be expressed as opposite responses with respect to energetic investment of the life history strategy – high-energy investment in rapid growth and dominance of space – K or C strategies, and/or high levels of reproduction – r or R strategies, and low-energy investment in longevity – K, or stress resistance – S strategies.

The literature on coral life history strategies has focused on life history traits such as recruitment rate, growth rate, colony size, colony morphology, longevity and reproductive strategies, with authors variously identifying 2 or 3 basic strategies (Table 1). Obura (2001) interpreted these with respect to bleaching patterns to distinguish the high-energy and low-energy options above, but an explanatory framework explaining why this should be so has been lacking. Obura (2009) proposes bleaching as a last-resort mechanism that the coral-zooxanthellae holobiont uses to manage energy relations consistent with the above strategies, and this paper explores this framework for understanding variability in bleaching patterns across taxonomic, spatial and temporal domains.

Methods

The hypothesized role of bleaching is to slow down zooxanthellar photosynthesis as an adversity response under stress, acting as a Stress Response Syndrome or General Adaptive Mechanism (Stebbing 1981). Explicit gene-environment interactions and selective pressures on bleaching as an SRS/GAM can be deduced and tested, against predictions for growth/reproduction or stress resistance based on life history theory (Stearns 1992). In scleractinian corals, growth and reproductive output are determined by zooxanthellae production and translocation rates, as these are energy intensive processes. Thus a direct relation between bleaching and reduced growth/reproduction can be inferred and used to interpret tradeoffs in life history strategies between high production (growth, reproduction) vs. stress resistance (persistence, adversity).

The paper will analyze hypothetical changes from a baseline state of a coral-zooxanthellae holobiont in the parameters of the bleaching response – the induction and maximum thresholds and counteractive capacity. Two basic responses of the bleaching parameters will be explored:

- A. Linear shifts up and down the stress gradient of induction and maximum thresholds, maintaining constant counteractive capacity (slope and range from induction to maximum), and
- B. Non-linear shifts up and down the stress gradient of induction and maximum thresholds, resulting in varying counteractive capacity, of the bleaching response.

These changes represent selective pressures imposed by environmental conditions on different life history strategies, and the hypothesized impacts on bleaching and holobiont survival will be analyzed for consistency with field observations and life history theory.

Results

A linear shift up or down the environmental axis, of both induction and maximum bleaching thresholds results in no change in the slope of the response, and no change in its counteractive capacity (Fig. 2a, Table 2). The resulting new bleaching responses are therefore:

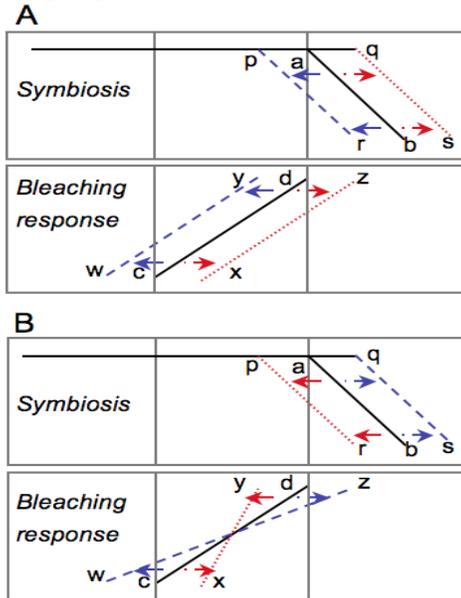


Figure 2. Bleaching response and symbiosis state – linear (A) and non-linear (B) shifts in response thresholds. Solid lines represent initial state, dotted lines are adaptive responses, see text and Table 2 for details.

Table 2. Summary of bleaching response and symbiosis states from Fig. 2, and see text for details.

Bleaching response	Symbiosis state	Growth rate	Stress resistance	Response shift
w-y	p-r	slow	low	Linear
x-z	q-s	fast	high	Linear
x-y	p-r (<r?)	fast	low	Narrowed?
w-z	q-s (>s?)	slow	high	Broadened?

- down-shift on the environmental axis (bleaching response c-d to w-y; symbiosis response a-b to p-r). The effect of this is less growth (earlier shut-down of maximum growth at w-y vs. c-d) and lower resistance to environmental stress (bleaching and mortality at lower levels of external stress p-r vs. a-b).
- up-shift on the environmental axis (bleaching response c-d to x-z; symbiosis response a-b to q-s). The effect of this is more growth (later shut-down of maximum growth at x) and higher resistance to environmental stress (bleaching and mortality at higher levels of external stress x-z vs. c-d and q-s vs. a-b).

Linear shifts in the bleaching response thus result in high growth-high stress resistance (x-z/q-s) and low growth-low stress resistance (w-y/p-r) strategies. Applied to a hypothetical environment (Fig. 3), the linear shifts correspond to shifts between the paired induction/maximum thresholds A-C and B-D.

Non-linear shifts up or down the environmental axis, of induction and maximum bleaching thresholds result in changes in the slope of the bleaching response, i.e. a change in the counteractive capacity (Fig. 2b, Table 2). The simplest non-linear responses are:

- down-shift of the bleaching induction threshold (c to w) paired with no change or up-shift in the maximum threshold (stable at d, or d to z). The effect of this is less growth (earlier shut-down of maximum growth at w) but a broader counteractive capacity, w-d or w-z, and potentially higher resistance to environmental stress if the maximum threshold increases to z. The corresponding symbiosis shift is from a-b to p-b, or to p-s.
- up-shift of the bleaching induction threshold (c to x) paired with no change or down-shift in the maximum threshold (stable at d, or d to y). The effect of this is more growth (later shut-down of maximum growth from c to x) but a narrower counteractive capacity, x-d, and potentially less resistance to environmental stress if the maximum threshold is reduced, x-y. This reduction in the maximum threshold may happen as a result of higher stress due to greater internal metabolic imbalance at the higher environmental stress levels. The corresponding symbiosis response is p-b, or even p-r.

Non-linear shifts in the bleaching responses, result in high growth-low stress resistance (x-y/p-r) and low growth-high stress resistance (w-z/q-s) strategies. Applied to a hypothetical environment, the non-linear shifts correspond to paired induction/maximum thresholds A-D and B-C (Fig. 3).

Other non-linear shifts may be possible, however these can all be expressed as variants on the above two options based on whether the bleaching response curves intersect (basic non-linear response above) or not (basic linear response above).

Discussion

The selective pressures that result in non-linear shifts can be described as follows. A shift in the induction threshold for bleaching, from c to w or x will result in earlier and later induction of bleaching (respectively). If environmental stress stays within that range, then a species with threshold x will always outcompete a species with threshold w, as all other things being equal, growth of species “x” will be unimpaired by bleaching, while growth of species “w” will decrease due to lower zooxanthellae density and production once c has been crossed. If there is no change in the maximum threshold

for bleaching, d , then species $x-d$ will always outcompete species $w-d$. This effect would be increased if a linear shift (Fig. 2a) were to occur (i.e. $x-y$ and $x-z$, respectively). Such shifts are incompatible with life history theory as tradeoffs in resource allocation prevent positive correlation between high growth and stress resistance (Stearns 1989, Hoffman and Parsons 1989). In any community if there is a species or genotype that could grow fastest and always resist stress, it would always dominate.

Tradeoffs imposed by life history options require that shifts in the bleaching induction threshold up or down are complemented by an opposite shift in the maximum thresholds, such that the species with induction threshold x will tend towards maximum threshold y and species with induction threshold w will tend towards maximum threshold z . This allows for a change in competitive advantage between the species once the environmental stress has exceeded the point at which the bleaching responses intersect (Fig. 2b). Below the intersection the fast-growing species $x-y$ will dominate, but above the intersection the stress resistant species $w-z$ will dominate.

Growth/production maximizers (x-y/p-r)

These species will tend to maximize utilization by the host of fixed products from the zooxanthellae and may also include maximization of production by zooxanthellae. They are dependent on their high growth (or reproductive) rate for competitive success and extension over space. Their tradeoff is a high opportunity cost of reducing production. Thus they may adapt to raise the induction threshold of their bleaching response to postpone decreased production. If conditions deteriorate further, bleaching will occur, and it is possible that tissue damage may be higher as a result of the raised induction threshold and higher levels of internal metabolic stress. This raised internal stress may narrow the counteractive capacity, effectively lowering the maximum threshold and bringing on earlier collapse of the symbiosis.

In a model environment, growth/production maximizers will have induction and maximum bleaching thresholds at B and C, respectively (Fig. 3). If environmental conditions stabilize before the induction threshold (E1), or perhaps at mid-levels in the bleaching response, the strategy is successful. However the lowered maximum threshold means they are more vulnerable where conditions do not improve or in highly fluctuating environments (E2) so have a high risk of mortality. These species thrive and dominate space in habitat

E1, outcompeting other species, but suffer high mortality in E2.

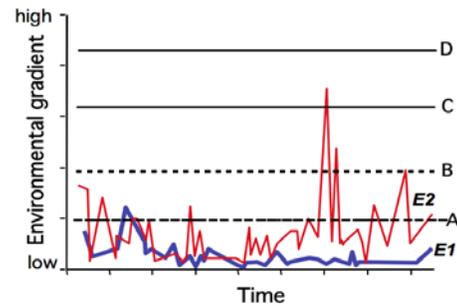


Figure 3. Environmental variability in benign (E1) and extreme (E2) habitats over time. Induction (horizontal lines A, B) and maximum (C, D) thresholds of a bleaching stress response (see Fig. 2) are shown. See discussion for details.

Stress tolerators/persisters (w-z/q-s)

These species will tend to minimize overall metabolism and therefore also production by zooxanthellae, and emphasize efficient use or management of fixed products by the host. They are dependent on their ability to persist under adverse conditions to maintain their space. Their tradeoff is low performance under good conditions. With a low opportunity cost of reducing production, early response to stress may develop. If this decreases the buildup of internal stress it may have the effect of broadening the range over which bleaching occurs, raising the maximum threshold that can be tolerated. This will further broaden the counteractive capacity and delay collapse of the symbiosis.

In a model environment, stress tolerators will have induction and maximum bleaching thresholds at A and D, respectively (Fig. 3). Under consistently benign conditions (E1), they cannot compete with production maximizers as they grow slower, and suppress growth at lower environmental stress levels. However, their higher maximum thresholds mean they can persist in widely fluctuating habitats (E2), with a low risk of mortality. These species persist in habitat E2, but are outcompeted by other species in E1.

These strategy descriptions fit classical life history strategies, both for r/K strategies and C-S-R strategies (Table 1), with the caveat that competitive and opportunistic strategies are both high growth/high risk strategies, but are optimized to different environmental conditions. With respect to bleaching and thermal stress, differences between ‘winners and losers’ have been described (e.g. Loya et al. 2001), explained by aspects of gross morphology, such as colony shape and tissue thickness. The analysis here offers an alternative framework based on metabolic rates and growth/resistance strategy, and further research may be able to show if growth form and other variables may be correlates or secondary to these. Certainly growth form

Table 3. Bleaching strategies summarized from Obura (2001) applied to life history strategies discussed in this paper.

Bleaching strategy	High bleaching/high growth	Variable bleaching/mortality	Persistent bleaching/low mortality
Bleaching observations	Severe bleaching response followed by near-100% mortality. Low stress resistance. Species generally fast growing and opportunistic. <i>Acropora</i> , <i>Pocillopora</i>	Graduated bleaching response with pale tissue, moderate mortality and recovery. Moderate to high stress resistance. Species generally slow growing, some large.	Persistent bleaching, low mortality. Moderate to high stress resistance. <i>Porites</i> , <i>Turbinaria</i> , <i>Astreopora</i> .
Life history strategy	Competitive and opportunistic	Intermediate/variable	Stress/adversity resistance

is a function of growth rates, where rapid growth is only possible for high surface area:volume growth forms such as branches and thin plates, and reproductive output is a direct function of capacity for photosynthetic output, egg production and tissue area. Branching corals are clearly the most susceptible to severe bleaching and to mortality following bleaching (Table 3) (Loya et al. 2001, Obura 2001, McClanahan 2004), while slow growing massives of both small and large sizes are the most stress resistant species (Table 1). Other variables such as tissue thickness are less clear in this regard, and further research may reveal a link.

In building up evidence for or against this hypothesis, the considerable variability in bleaching responses, and in the first-order responses that may dramatically alter the induction and appearance of bleaching, must be carefully considered. For example, a straightforward interpretation would state that stress tolerant corals would bleach earlier but more mildly than fast growing corals (Figs. 2 & 3). This can be seen in some cases of seasonal bleaching where small and large *Porites* massive colonies in lagoon reefs in East Africa often bleach at temperatures in the local spring (rapidly rising but intermediate temperatures in November) that don't cause bleaching in more susceptible species (pers. obs.). But during local-summer bleaching the first corals to bleach are usually the competitive and opportunistic genera. As expected though, they do tend to bleach more severely (steep response curve) and suffer mortality early. It may be that many of the pre-bleaching stress responses (Obura 2009) in stress tolerant corals are also tuned to an adversity response such that they effectively minimize internal stress thus pushing the bleaching induction threshold farther up the stress gradient than suggested by Figs. 2b and 3 with a combined effect of raising the maximum bleaching threshold.

The complex interactions and multiple stress responses in coral-zooxanthellae symbiosis (Brown 1997) contribute to variability in observed responses and explanations of bleaching (Coles and Brown 2003, Hoegh-Guldberg 2005) and a broad phase-space of bleaching-mortality dynamics (McClanahan 2004). As noted by Douglas (2003)

this argues against overly-deterministic attempts to explain bleaching in terms of single phenomena. This life history model based on whole-organism emergent behaviour (Obura 2009) helps to identify patterns of acclimatization and adaptation above the detail of individual mechanisms that are precursors to the bleaching response itself.

References

- Bak R, Engel M (1979) Distribution, abundance and survival of juvenile hermatypic corals (Scleractinia) and the importance of life history strategies in parent coral community. *Mar Biol* 54: 341-352
- Brown B (1997) Adaptations of Reef Corals to Physical Environment Stress. *Adv Mar Biol* 31:222-299
- Cameron AM, Endean R (1985) Do long-lived species structure coral reef ecosystems? *Proc Fifth Int Coral Reef Congr* 6: 211-215
- Coles S, Brown BE (2003) Coral bleaching - capacity for acclimatization and adaptation. *Adv Mar Biol* 46: 183-224
- Douglas AE (2003) Coral bleaching-how and why? *Mar Pollut Bull* 46: 385-392
- Fautin DG, Buddemeier RW (2004) Adaptive bleaching: a general phenomenon. *Hydrobiologia* 530/531: 459-467
- Greenslade P (1983) Adversity selection and the habitat templet. *Am Nat* 122: 352-365
- Grime J (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am Nat* 111: 1168-1194
- Hoegh-Guldberg O (ed) (2005) Understanding the Stress Response of Corals and Symbiodinium in a rapidly changing environment ICMyL, UNAM. <http://www.gefcoral.org/Portals/25/Mexico%20>
- Hoffman A, Parsons P (1991) Evolutionary Genetics and Environmental Stress. Oxford University Press, Oxford. 284pp
- Jackson J, Hughes T (1985) Adaptive strategies of coral-reef invertebrates. *Am Sci* 73, 265-274
- Kojis B, Quinn NJ (1984) Seasonal and depth variation in fecundity of *Acropora palifera* at two reefs in Papua New Guinea. *Coral Reefs* 3: 165-172
- Loya Y, Sakai K, Yamazato K, Nakano Y, Samabali H, van Woesik R (2001) Coral bleaching: the winners and the losers. *Ecol Lett* 4: 122-131
- MacArthur R (1960) On the relative abundance of species. *Am Nat* 94: 25-36
- McClanahan T (2004) The relationship between bleaching and mortality of common corals. *Mar Biol* 144: 1239-1245
- Obura DO (2001) Can differential bleaching and mortality among coral species offer useful indicators for assessment and management of reefs under stress? *Bull Mar Sci* 6: 421-442
- Obura DO (2009) Reef corals bleach to resist stress. *Mar Pollut Bull* 58:206-212
- Pianka E (1970) On r- and K-selection. *Am. Nat.* 104: 592-597
- Stearns S (1989) Trade-offs in life-history evolution. *Funct Ecol* 3, 259-268
- Stearns S (1992) The Evolution of Life Histories. Oxford University Press, Oxford.
- Stebbing ARD (1981) Stress, health and homeostasis. *Mar Poll Bull* 12, 326-329