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The Adaptive Hypothesis of Bleaching

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1. Introduction

1.1 Biological Background

Despite the perception that corals and coral reefs are limited to stable habitats distinguished by very narrow environmental parameters, the coral-algal symbiosis is capable of surviving in a variety of extreme conditions. Through the process of photoadaptation, corals and their algal symbionts adjust algal densities and pigment concentrations to function over a wide range of light levels ranging from direct exposure

to full sunlight in intertidal corals to virtual darkness at the extreme limits of the photic zone (>200m) on reef slopes (Zahl and McLaughlin 1959, Schlichter et al. 1986). Corals and reef communities in some areas (such as the Arabian Gulf) tolerate salinity and temperature conditions that are lethal when imposed rapidly on the same species in less extreme environments (Coles 1988, Sheppard 1988, Coles and Fadlallah 1991, Jokiel this volume). There are abundant reports of reef corals occurring in turbid, high nutrient, nearshore habitats (Larcombe et al. 2001). Coral reefs exist at the inherently variable interface between the sea, air and land (Smith and Buddemeier 1992), and reef communities have persisted over geological time through significant climate and sea-level fluctuations. Despite this, rates of speciation and extinction in scleractinian corals have been relatively low over the last 220 million years (Veron 1995).

Because the mechanisms by which reef corals adjust to these diverse environments are only poorly understood, we have little basis for estimating or predicting actual or potential rates of adaptive change. This issue is of particular interest because of the present high rates of coral mortality and reef degradation (e.g., Hoegh-Guldberg 1999, Wilkinson 2000) caused in substantial measure by the two large-scale threats of bleaching and other diseases.

1.2 Conceptual background

Three lines of evidence concerning coral-algal symbioses converged in the early 1990s, concurrently with rising concern over the increasingly widespread phenomenon of frequent and severe coral bleaching. One line of evidence derived from molecular studies of the algal symbionts (often referred to as zooxanthellae) in scleractinian corals that revealed extraordinary diversity in the genus *Symbiodinium* (Rowan and Powers 1991). These findings reinforced the significance of the second line of evidence, consisting of earlier reports that various types of symbiotic algae could form metabolically different symbioses with the same host (e.g., Kinzie and Chee 1979). The third line of evidence arose from reports of variations in bleaching susceptibility, occurrence, and recovery (e.g., Oliver 1985, Jokiel and Coles 1990). Arguing for a consistent explanation for the combination of these observations, Buddemeier and Fautin (1993) proposed the “Adaptive Bleaching Hypothesis” (ABH). A basic precept of the ABH is that changing

combinations of hosts and symbiotic algae have the potential to create “new” ecospecies (see section 2.1) that differ in environmental tolerances. Diversity and flexibility of partnerships within a host organism, occurring over small spatial scales and short (single generation) timescales, could explain differences from one population to another of corals (for example, in bleaching threshold temperature: e.g., Coles et al. 1976, Coles and Jokiel 1977). Buddemeier and Fautin (1993) interpreted these observations as evidence of differences in the ecospecies (see section 2.1): what appeared in each case to be a single coral species was physiologically not the same.

Ware et al. (1996) used a simple competition model to explore the parameters underlying the ABH, and emphasized that disturbance frequency is an important factor in determining possible outcomes. Subsequently, Buddemeier et al. (1997) placed the ABH in the context of a more conventional, but still very rapid, form of adaptation, based on the potential for somatic mutation to produce genetic chimeras in colonial corals. In such chimeras, selection could potentially act on multiple animal genotypes within a single colony, with each animal genotype possibly interacting with a different type of photosymbiont. Beginning in 1999, the widespread application of molecular methods to identify algal symbionts, combined with increasingly intense bleaching events worldwide following the 1997-98 El Niño, led to a relatively sudden proliferation of studies relating to the ABH, its mechanisms, or its underlying assumptions.

1.3 Aim and scope

The purpose of this paper is to update the relevant literature, and to review some basic features of the ABH in order to clarify some confusion and misunderstanding that has become apparent since the original phrasing of the hypothesis.

The ABH has clear relevance for coral symbioses involving both eukaryotic and non-eukaryotic microbes. Accordingly, discussions of the relevance of the ABH to continued coral health can be framed in the context of both coral bleaching and microbial and viral pathogenic disease (which may initiate or be initiated by bleaching). The microbial community associated with corals is diverse and complex, having features in common with the coral-algal symbiosis (Rohwer et al. 2001, 2002; Knowlton and Rohwer in press). As is the case with the bleaching of endosymbiotic algae,

environmental change may elicit compensatory change in microbial symbiont communities that shift the degree to which each partner benefits from and contributes to the symbiosis.

2. Adaptive Bleaching: Characteristics and Definitions

2.1 Terminology

We use the term "ecospecies" to refer to any combination of host and symbiont(s). The introduction of this term implicitly assumes that conspecific hosts with different complements of symbionts (or conspecific symbionts in different hosts) may, and in at least some cases will, differ in environmental tolerances. It does not necessarily imply that each partner is a single entity; since multiple symbiont taxa may occur at different relative abundances within a single host, one functional ecospecies may differ from either in kinds or in relative proportions of symbionts.

The ABH infers mechanisms from phenomena, rather than deducing outcomes from known mechanisms. One of the major phenomena under consideration is “adaptation” in the vernacular (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..." (Webster's Ninth New Collegiate Dictionary). Mechanistically this may subsume any combination of what biologists define as acclimation, acclimatization, or adaptation. A change in ecospecies is a biological adaptation in the sense that the genetic composition of the holobiont is altered, but this adaptation involves neither speciation nor extinction, and occurs over very short timescale (within the lifetimes of the partners).

2.2 Diversity in taxonomy, scale, and environment

The diversity of organisms involved, their differences in selectivity and mode of acquisition of symbiotic partners, and the degree to which their associations are obligate or facultative (Figure 1) preclude easy generalizations from experimental observations in a limited number of organisms or locations. Experimental tests are necessary, but are of limited power individually.

Moreover, the symbiotic or physiological characteristics of any given ecospecies are not necessarily directly predictable from observations made on individual partners in isolation (*e.g.*, in culture) or in other combinations. Distinguishing ecospecies from one another is further complicated by uncertainties in determining functional diversity of symbionts from (predominantly molecular) systematic data. Unambiguous identification of hosts can also be problematic. In the case of scleractinian corals, hybridization and reticulate evolution (*e.g.*, Veron 1995; van Oppen et al. 2000, 2002), and potentially rapid rates of somatic mutation (Buddemeier et al. 1997, Fautin 1997) may result in functionally different but taxonomically indistinguishable populations or individuals of the same apparent “species.”

In addition to taxonomic uncertainties, there are uncertainties about the relationships among the environmental parameters that humans measure and the environment to which the ecospecies respond, and to which they are or are not adapted. Temperature and light (or proxies such as latitude and depth) are the variables most commonly investigated, but water motion (Nakamura and van Woesik 2001), water quality (including salinity and nutrients; *e.g.*, Fagoonee et al. 1999), and possibly predation (Augustine and Muller-Parker 1998) all contribute to the environmental conditions experienced by intact associations. In addition, bacterial and viral communities present in these associations may constitute an important environmental component affecting the symbioses (see chapters by Smith, Bythell, and Rohwer, this volume). Interpreting environmental gradients in the context of single- or dual-variable changes could oversimplify the real picture.

The ABH can be envisioned as a process operating at either of two environmental end-members, or along a continuum between them. One end-member is a discrete change in environmental state, such as might occur with a climate-driven shift in major current patterns, or by alteration of lagoonal flushing and circulation due sea-level change crossing a threshold datum. Since the baseline condition is changed, a new and more favorable ecospecies formed in response to the stress at the onset of the new condition is likely to persist. By contrast, a stress and recombination event followed by return to the previous norm has a higher probability of reverting to the previously stable ecospecies. The transplantation experiments of Baker (2001) represent a step-function change, in

contrast to many of the laboratory experiments that have compared the relative stability of homologous and heterologous infections under conditions known to be suitable for the homologous ecospecies.

The other end-member type of environmental change consists of rapid oscillations around a stable baseline of environmental conditions. Adaptation in this case is not to average conditions, or even to average conditions between stress (e.g., bleaching) events, but primarily to the frequency and intensity of stresses. This is exemplified in some of the model results of Ware et al. (1996).

In nature, environmental change can partake of both characteristics; at present, climate change is changing baseline conditions at rates that are relatively rapid on the scale of at least some host species' lifetimes, and concurrently the present enhanced ENSO regime is imposing higher frequencies and intensities of extreme conditions than has been the case in the past. These phenomena are not the same, or even necessarily related, and they may put organisms and symbioses under different but concurrent selective pressures.

2.3 Stochasticity

Figure 2 illustrates the diverse mechanisms and processes that might be involved in adaptive bleaching. We use the analogy of a lottery to describe how chance may play an important role in determining the types of algae available to, and taken up by, potential hosts once the need or opportunity to re-equilibrate symbiotic relationships arises. Here we consider only the odds of winning on a single lottery ticket; the question of how many tickets are purchased, or how often, is considered in the preceding section as part of the question of frequency and intensity of disturbance.

Some partners may be highly selective, or may be limited by modes of symbiont transmission or infection that make them ineligible to participate in the algal lottery at a given time or place. For those that do have a chance in the lottery, variations in abundance and condition of potential partners and in external (environmental) conditions determine the probabilities of successfully obtaining new algae that are either the same as or different from the previous (dominant) type(s). However, distinguishing internal proliferation of existing symbiont populations from *de novo* acquisition of symbionts

from the environment is difficult or impossible in most cases, and is immaterial to whether the ABH operates.

A particular bleaching event is not necessarily adaptive for any given individual because adaptive characteristics may be detectable only at the population scale. Adaptive change may occur over the course of multiple repetitive stress events, and may take several generations to become established at the community or ecosystem level. For this reason, the ABH is not readily falsifiable by limited individual observations – most specific cases will probably not document “adaptation” by recording change in symbiotic partnerships. Although unsatisfying for the experimental ecologist, this simply reflects the processes and scale of operation of this phenomenon.

Figure 2 also illustrates that significant change in the dominance of symbiotic algae types in hermatypic corals can routinely occur in the absence of observable bleaching or stress (*e.g.*, Gates 1990, Fagoonee et al. 1999, Brown et al. 1999, Fitt et al. 2000; see also section 4.2). Such shifts may occur in corals with multiple types of algal symbionts as a result of gradual environmental change, or of gradual competitive takeover by an alga that is slightly better suited to a stable environment than its co-symbionts. Similar fluctuations in symbiont populations occur in tropical sea anemones, but apparently not in their temperate counterparts (reviewed by Muller-Parker and Davy 2001). Although the mechanisms and outcomes would be those of the ABH, a focus on routine rather than extraordinary transitions between ecospecies would emphasize rather different ecological and evolutionary implications. The ABH was initially conceived to explain two obvious features of coral reefs and reef coral biology: the paradox of reefs seeming robust in the long term but fragile in the short term; and what seems on its face a maladaptive response to trauma -- the breakdown of a vital mutualism. Obvious bleaching may simply be an extreme manifestation of a mechanism that allows both partners to track the environment by continually making adjustments that shift ecospecies. Focus on the coral -- and especially on the skeleton -- gives the impression that change is slow and rare. Now that we can differentiate members of the other element in the symbiosis, we can assess the critical element, the ecospecies.

3. Accumulating Evidence

3.1 Taxonomic and functional diversity

3.1.1 Hosts

Particular attention has been paid to scleractinian corals in the context of bleaching and climate change because contemporary reefs are formed predominantly by about 750 species of this group (Veron 2000). However, sea anemones, soft corals, hydrozoans, bivalves, foraminifera and possibly sponges are also hosts to various types of *Symbiodinium* that are in many cases indistinguishable from those found in scleractinian hosts. Thus, a conservative estimate of the number of animal taxa that serve as hosts for endosymbiotic algae would be on the order of a few thousand; these occupy a wide range of habitats and form the reservoir of algal types for potential exchange and repopulation.

Multiple hosts, multiple types of algae (even within single host species) and the diverse habitats in which these organisms are found suggests a diverse reservoir of symbiotic algae types in almost every region where symbiotic organisms are common.

3.1.2 Symbiotic algae

Since the original proposal of the ABH, the number of distinct types of *Symbiodinium* has expanded at an accelerating rate (see Baker (in press) and Baker (this volume) for review). Rowan and Powers (1991) initially documented five or six types in three clades identified as A, B, and C, with between-clade genetic distances comparable to those between some non-symbiotic dinoflagellates in different orders. In less than ten years, distinctions rose to 10-20 types (Rowan 1998, Baker 1999), and then, in less than another five years, to 50-60+ types (Baker this volume, LaJeunesse 2002, Santos et al. 2002, Pochon et al. 2001, Carlos et al. 1999). Additional diversity clearly remains to be documented as both sampling and analytical techniques are further refined. Thus, an inventory on the order of hundreds of distinguishable taxa is probably not unrealistic in the near future. Rowan's (1998) remark that our estimates of diversity probably represent minima is as true now as when he wrote it: "*By these methods [rDNA analysis], the observed*

number of taxa is a minimum estimate of the actual number and failure to reject the null hypothesis ['symbionts collected within one host species are not different'] cannot be regarded as evidence to support it."

Another challenge is distinguishing functionally different subpopulations. Some studies using relatively conserved molecular methods have failed to resolve algal taxa that clearly differ functionally in terms of their response to environmental parameters (Kinzie et al. 2001, Savage et al. 2002b). However, Santos et al. (2002), using relatively variable chloroplast gene sequences to identify functional subpopulations described by Kinzie et al. (2001), found that cultures with the same responses had identical sequences, while distinctive responses were associated with unique sequences.

3.2 Existence of distinguishable, changeable partnerships

3.2.1 Availability and infectivity of algal symbionts

Current evidence indicates that ambient algae populations exist in seawater (Kinzie et al. 2001, Y. Benayahu this volume, F. Rohwer pers. comm.), that even recently expelled algae may remain sufficiently competent to participate in the algal lottery depicted in Figure 2 (Ralph et al. 2001, Perez et al. 2001), and that there are vectors for transmission of algae to bleached hosts (Muller-Parker 1984).

Laboratory studies have demonstrated that aposymbiotic (bleached) hosts can become infected with "heterologous" symbionts isolated from hosts of other species (Kinzie 1974, Kinzie and Chee 1979, Schoenberg and Trench 1980, Colley and Trench 1983, Fitt 1985, Davy et al. 1997, Toller et al. 2001b, Kinzie et al. 2001), thereby establishing that a single host can associate with various symbionts. Selectivity in these partnerships, however, may exist (Weis et al. 2001), and by analogy with other symbioses, it is likely that certain combinations of hosts and symbionts are impossible.

Field studies have detected multiple symbiont taxa individual coral colonies as well as within single host species (LaJeunesse 2002, Carlos et al. 2000; Darius et al. 2000; Baker 1999, Goulet and Coffroth 1997; Rowan et al. 1997; Baker et al. 1997, Rowan and Knowlton 1995, Toller et al. 2001b). A single coral species may host different complements of algal symbionts in different parts of its geographic range (van

Oppen et al. 2001, Loh et al. 2001, Rodriguez-Lanetty et al. 2001), or have the same suite of algae, but in different ratios. This diversity is often distributed over predictable environmental gradients, particularly light. Rowan (1998) suggested that "...polymorphic symbioses may be a common feature of holobiont biology."

An important caveat in discussing diversity is the potential for discrepancy between freshly separated and cultured algal symbionts (e.g., Rowan 1998, Carlos et al. 1999, Toller et al. 2001, LaJeunesse 2002, Santos et al. 2001). LaJeunesse (2002) stated that "...in most instances the cultured type is not the symbiont that populates the host in nature...hosts may contain low abundances of *Symbiodinium* spp. not detected by current molecular methods." The apparently low abundance of unusual types of *Symbiodinium* found in many hosts may be the result of laboratory parallels of the concept of adaptive bleaching during the culture process. Differential inoculation of *Symbiodinium* into culture or differential success of algal symbionts in culture (like the infection or acquisition of different symbionts by different hosts), combined with environmental conditions during culture that differ between experiments or laboratories (notably temperature and light: Kinzie et al. 2001, Rowan 1998), can control competitive interactions to allow the emergence of what had been minor symbionts *in vivo* as dominants *in vitro*.

The important question of the spatial distribution of multiple concurrent symbionts, especially for minor types, is not resolved. Rowan et al. (1997) provided dramatic illustration of niche partitioning by different algal symbionts within the same host. In this case, as in other studies of within-colony microhabitats, three distinct *Symbiodinium* taxa occupied distinct irradiance zones within the host colony. Macroscopic separation has also been studied in sea anemones, which do not form colonies: in a species symbiotic with both a chlorophyte and *Symbiodinium*, proportions of the two photosymbionts in an anemone differs with intertidal height (McCloskey et al. 1996, Bates 2000). Within individual anemones, proportions of the same two photosymbionts vary systematically as a function of location; the ratio of *Symbiodinium* to chlorophyte is systematically higher in the tips of tentacles than at their bases, and in the oral disc compared to the column (G. Muller-Parker, pers comm.) Whether populations of algal symbionts are separated or intermingled has very different implications for algal

competition and dominance shifts. Spatial patterning implies that the algae assort or are assorted in response to environmental parameters and the potential for direct competition is minimal, whereas microsympatry implies the opposite.

The widely-held view that there is exclusive host and/or algal specificity is not representative of many symbioses, and the degree to which strictly specific symbioses may exist is not yet known. Most symbiotic systems appear to exhibit a range from specialists to generalists in both (all) partners, so it is reasonable to assume that some strictly specific relationships will be found. Studies that have reported a single symbiont taxon occurring in a given host species (Belda-Baillie et al. 2002; Coffroth et al. 2001, Diekmann et al. 2003) have often relied on relatively low-resolution rDNA analyses that are imprecise in their identifications.

Additionally, there is evidence of hosts that can associate with several symbiont types as juveniles, but only one type as adults. Coffroth et al. (2001) found that juveniles of the octocoral *Plexaura kuna* could simultaneously associate with several symbionts, but individual adults appear to host just one, although that type varies from individual to individual (Goulet and Coffroth 2003). The evidence that hosts will phagocytize algae of at least several types suggests that if there is recognition of particular types by the host, it occurs after the symbiont enters a host cell (Schwarz et al. 2002).

3.3 Characteristics of ecospecies

3.3.1 Existence of environmental/geographic gradients

Environmental correlates of symbiont distributions and differences in sensitivity to stress-induced bleaching have been observed since the mid-1990s. Initial studies in the Caribbean suggested that in the *Montastrea* species complex, members of *Symbiodinium* in clades B and C were "sun" and "shade" specialists, respectively (Rowan and Knowlton 1995, Rowan et al. 1997), and members of clade A were stress-insensitive and weedy (Rowan 1998, Toller et al. 2001b). Extension of this work (Baker 1999, Toller 2001a, LaJeunesse 2002) revealed additional symbiont taxa exhibiting ecological distributions in the Caribbean, although some site- and/or taxon-specific studies

(Diekmann et al. 2002, Savage et al. 2002b) found no consistent environmental correlates.

In the tropical Indo-Pacific, initial observations of the ubiquity of clade C (Baker and Rowan 1997, Baker 1999) have been supported (Loh et al. 1998, Pochon et al. 2001, Van Oppen et al. 2001, LaJeunesse et al. 2003, Baker in press), but with increasing recognition of the occurrence of an additional clade (D) and of significant diversity within C. In the western Pacific, multiple geographic and systematic surveys have revealed both biogeographic and habitat- or host-specific distribution patterns for symbiont types (van Oppen et al. 2001, Loh et al. 2001, Rodriguez-Lanetty et al. 2001). In addition, emerging evidence suggests that clade D is relatively stress-resistant (Baker 1999, Van Oppen 2001, LaJeunesse 2001), dominates in extreme environments, and tends to replace members of clade C in Indo-Pacific areas such as the eastern Pacific and the western Indian Ocean that have been affected by severe bleaching episodes (Baker in press and this volume).

3.3.2 Evidence for ecospecies transitions

It has been shown that unusual host-algal symbiont combinations can become established following bleaching (e.g., Toller et al. 2001b), that both algae and the ecospecies they form with various hosts can be associated with specific environmental conditions or habitats, and that the individual mechanisms required for the ABH to function exist and operate in nature (this review, but see also Kinzie et al. 2001). A null hypothesis of the ABH could be framed as: "Hosts that recover from bleaching will always have the same type(s) of algal symbiont(s) (in the same proportions) as before the bleaching." This hypothesis has clearly been falsified. However, while data demonstrating the potential of the ABH and providing support for its existence have been reported, detailed demonstration of its importance or occurrence in the field is more difficult to obtain.

Field data indicate that El Niño-related bleaching on eastern Pacific reefs was much worse during the 1982-83 event than the 1997-98 event, even though temperature excursions during the two events were similar (Guzmán and Cortés 2001, Podestá and Glynn 2001, Glynn et al. 2001). Although factors other than temperature also affect

bleaching, the difference in responses to these two events supports the general idea that corals can adapt to higher temperatures over decadal time scales, either through adaptive bleaching or through evolutionary selection for more heat/irradiance-tolerant individuals that survive bleaching events (Baker 2002, in press). That symbiont communities play a role in this adaptation is demonstrated by the observation that the regionally dominant algal clade had shifted from C to D over the course of the observations (Glynn et al. 2001).

In a field transplant experiment, Baker (2001) demonstrated that corals could bleach and recover with different *Symbiodinium* communities that were more suited to the new environmental conditions. There are also in progress some field studies and monitoring efforts (various pers. comm., Fitt unpubl., Baker unpubl.) with promise to provide colony-specific observations over time, but these have not yet reached the stage of publication.

4. Discussion and Development

4.1 The ABH in its original sense -- Evidence for existence

We argue that adaptive bleaching as originally proposed (Buddemeier and Fautin 1993) occurs to varying degrees and over varying timescales in various hosts. All of the most fundamental assumptions have been tested (Kinzie et al. 2001, Toller et al. 2001ab, Santos et al. 2002a), several specific mechanisms have been individually demonstrated (Fitt et al. 2000, 2001), and some persuasive (but not rigorously conclusive) examples of field adaptation have been reported (Baker 2001, Glynn et al. 2001). We suggest that the level of available evidence justifies its acceptance as a working hypothesis, with the proviso that its stochastic nature must be recognized -- it can be expected to function at the community and ecosystem level over multi-year scales, but it cannot provide deterministic predictions about the outcomes of specific events or the fate of individual specimens (or perhaps even taxa).

The immediate concern is the degree to which the ABH or its component features buffer reef systems against repeated stress episodes capable of inducing severe bleaching,

and the absolute limits to ecospecies adaptation by recombination. Coupled with, and underlying, this immediate issue is the question of the larger evolutionary and ecological roles of flexible, multi-partner symbioses and the inevitable range of flexibility and specificity they exhibit.

4.2. Symbiotic adaptation as a general phenomenon

Certain aspects of the ABH that were implicit in its original formulation have become more central to the hypothesis with the discoveries of the last decade. Growing evidence for concurrent multiple infections, with a variety of viable symbiont types existing at very low levels within many hosts, shifts emphasis from a narrow window of reinfection opportunity following recovery from bleaching, and changes the odds in the lottery of Figure 2 by suggesting that some hosts may be able to sample the environment and stockpile seed populations of alternative symbionts over time (the "moonlighting" symbionts of Baker in press).

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 (Fitt et al. 2000, 2001) may not be required for adaptive or acclimatory responses in ecospecies.

The ABH has occasionally been misinterpreted and misapplied as being a deterministic process, or one that is relevant only to major bleaching events that result in prompt acquisition of heterologous algae from the external environment. Growing evidence suggests that the ABH is a synthetic hypothesis that is based on a number of relatively well established processes that occur with some frequency in photosymbiotic invertebrates. It is timely and appropriate to seek a set of terms and concepts that will further understanding of both the theoretical and applied aspects of the role of symbioses, and especially of changeable or multiple symbioses, in adaptive, acclimative, and evolutionary processes.

5. Conclusions and Recommendations

5.1 Summary of conclusions

We offer the following summary conclusions from the foregoing review:

- There is abundant and rapidly expanding evidence for the existence of multiple types (taxa) of algal symbionts, with a wide range of host-systematic preferences and environmental optima;
- Many -- perhaps most -- hosts can support internal populations of multiple algal types, concurrently and/or serially. Transmission and/or infection mechanisms to establish these populations exist;
- The ecospecies concept, whereby different host-symbiont combinations exhibit different responses to environmental conditions, is strongly supported; and,
- The Adaptive Bleaching Hypothesis, as a stochastic process operating over large population scales, can be regarded as confirmed in principle, but future tests and applications of the hypothesis can most profitably be viewed as an introduction to the larger issues of ecospecies roles in evolution and ecology over multiple scales.

5.2 Unresolved questions and future research

5.2.1 *Photosymbiont and ecospecies issues*

Improvements in algal taxonomy, and especially the relationship between genetic and functional diversity, has greatly improved over the last decade, but remains a limiting factor in this research. Further surveys of the temporal stability of symbiotic associations in nature and of the taxonomic and environmental ranges of ecospecies and their component partners are needed.

Growing appreciation for the ecospecies concept suggests potential for a new generation of careful laboratory experiments to determine the physiological responses of different ecospecies and the underlying basis for documented examples from the literature (*e.g.*, Coles et al. 1976, Coles and Jokiel 1977). Such experiments would be

critical for understanding the fundamental environmental limits to symbiosis-based adaptation and acclimatization.

The actual nature, extent, distribution, and stability of multiple symbiosis with various types of photosymbionts needs further investigation, in large part because ecological interpretations of selectivity and specificity in patterns of distribution (*e.g.*, van Oppen et al. 2001, Loh et al. 2001, Rodriguez-Lanetty et al. 2001) may depend heavily on the relative importance of symbiont availability, partner preferences, and algal competitive advantages under various interacting combinations of environmental variables (Jacobs in prep.).

5.2.2 Disease and microbial symbiosis issues

This volume provides an important linkage between the conceptually parallel and functionally interrelated fields of algal and microbial symbiosis in coral reef invertebrates. Initial demonstrations of the role of microbes as causative agents of bleaching (Kushmaro et al. 1996, 1998; Ben Haim and Rosenberg 2002) and in the algal population responses to disease (Toller et al. 2002b) have provided some clues to the phenomenological links that may exist in the combined area of coral health, environmental stress, and disease.

Even more important for further development are the conceptual and process-based similarities in the acquisition, dynamics, and modulation of very different but interactive symbiont communities by the same hosts. The disciplines involved have different conceptual approaches and experimental strengths; combining them effectively has the potential to yield wide-ranging integrative breakthroughs.

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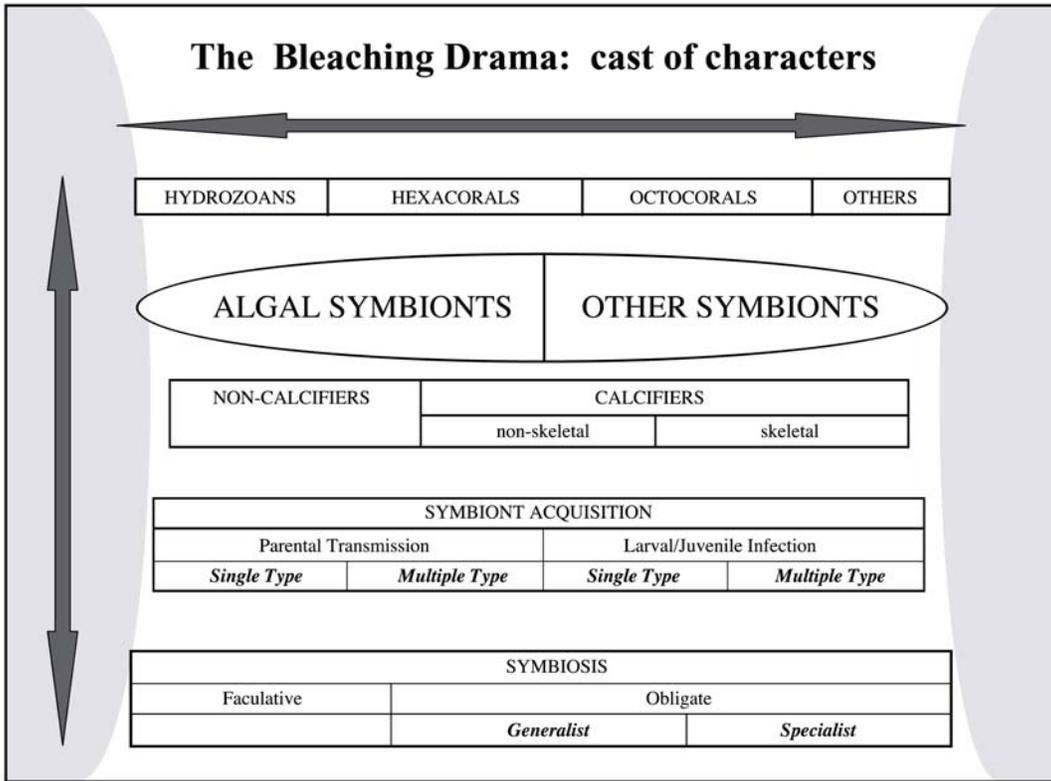
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Figure Legends

Figure 1: *Symbiodinium* is found in a wide range of phylogenetically diverse host taxa, including “corals” (in the broadest sense) and their cnidarian relatives, both calcifying and non-calcifying. In addition, bivalves, sponges, and foraminifers are also hosts (Trench 1992, Baker in press for review). Various hosts may be facultatively or obligately symbiotic, and hosts and algal partners may exhibit varying degrees of selectivity. These diverse hosts differ not only in structure, habitat and life history, but also in their modes of symbiont acquisition.

Figure 2: Illustration of potential processes involved in transition from an initial to a final (different) ecospecies, depending on the characteristics and history of the original ecospecies, the local ecosystem (availability of symbionts), and the characteristics of the environment over time. The stochastic nature of the process is emphasized, and some of the complexity illustrated in Figure 1 is omitted in the interests of relative clarity. The "reversion" process under stable environmental conditions interrupted only by occasional stress events is an example of an ecospecies transition that may occur without perceptible bleaching; it is discussed in section 2.3.

The Bleaching Drama: cast of characters



The ABH addresses stochastic processes with multiple pathways for recovery of surviving organisms

