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FLEXIBILITY AND SPECIFICITY IN CORAL-ALGAL SYMBIOSIS: Diversity, Ecology, and Biogeography of *Symbiodinium*

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"Whatever is flexible and flowing will tend to grow,
whatever is rigid and blocked will wither and die,"

—Tao Te Ching

■ **Abstract** Reef corals (and other marine invertebrates and protists) are hosts to a group of exceptionally diverse dinoflagellate symbionts in the genus *Symbiodinium*. These symbionts are critical components of coral reef ecosystems whose loss during stress-related "bleaching" events can lead to mass mortality of coral hosts and associated collapse of reef ecosystems. Molecular studies have shown these partnerships to be more flexible than previously thought, with different hosts and symbionts showing varying degrees of specificity in their associations. Further studies are beginning to reveal the systematic, ecological, and biogeographic underpinnings of this flexibility. Unusual symbionts normally found only in larval stages, marginal environments, uncommon host taxa, or at latitudinal extremes may prove critical in understanding the long-term resilience of coral reef ecosystems to environmental perturbation. The persistence of bleaching-resistant symbiont types in affected ecosystems, and the possibility of recombination among different partners following bleaching, may lead to significant shifts in symbiont community structure and elevations of future bleaching thresholds. Monitoring symbiont communities worldwide is essential to understanding the long-term response of reefs to global climate change because it will help resolve current controversy over the timescales over which symbiont change might occur. Symbiont diversity should be explicitly incorporated into the design of coral reef Marine Protected Areas (MPAs) where resistance or resilience to bleaching is a consideration.

INTRODUCTION

The unicellular algal symbionts found in reef corals and associated reef biota are critical to understanding the past evolution, present distribution, and future fate of coral reefs and the ecosystems they support (Cowen 1988, Hoegh-Guldberg 1999, Muscatine & Porter 1977). In fact, despite their fantastic abundance (a healthy coral reef might easily contain $>10^{10}$ algal symbionts per m^2), their relatively small overall biomass suggests these symbionts represent keystone species (Paine 1969, Power et al. 1996) on coral reefs—perhaps the only protists to play such a role.

Currently, eight genera in four (or five) classical orders of dinoflagellate are recognized as endosymbionts in marine invertebrates and protists (Banaszak et al. 1993, Trench 1997). *Symbiodinium* is the most studied genus in this paraphyletic group and is commonly found in shallow water tropical and subtropical cnidarians. These algae, commonly referred to as "zooxanthellae," are ubiquitous members of coral reef ecosystems (Rowan 1998, Taylor 1974, Trench 1993): Cnidarian species reported to contain *Symbiodinium* include many representatives from the class Anthozoa (including anemones, scleractinian corals, zoanthids, corallimorphs, blue corals, alcyonacean corals, and sea fans) and several representatives from the classes Scyphozoa (including rhizostome and coronate jellyfish) and Hydrozoa (including milleporine fire corals). *Symbiodinium* has also been identified from gastropod and bivalve mollusks [including tridacnid (giant) clams, heart cockles, and possibly, conch], large miliolid foraminifera (in the subfamily Soritinae), sponges, and a giant heterotrich ciliate (see Trench 1993 for review; Carlos et al. 1999; Lobban et al. 2002; Hill & Wilcox 1998; and references in Figure 1). However, in many of these groups, symbionts have only been definitively identifid from a few representatives; only a few groups (scleractinian corals, soritid foraminifera, gorgonians, and tridacnid clams) have been surveyed using molecular techniques to an extent that might be considered marginally representative (Baker 1999; Baker & Rowan 1997; Goulet 1999; LaJeunesse 2002; Pawlowski et al. 2001; Pochon et al. 2001; Rowan & Powers 1991a,b; Santos et al. 2002a).

It is clear that additional diversity in *Symbiodinium* remains to be discovered (Baker 2003) and that most species are uncultured and undescribed (Rowan 1998, Santos et al. 2001). Many records of "zooxanthellae" present in invertebrates are based on only cursory observations or anecdotal reports. Moreover, in addition to the dominant populations of symbiotic dinoflagellates in these hosts, many unusual or novel variants may also occur as cryptic and unstable transients whose physiological or ecological importance is not yet clear (Goulet & Coffroth 1997, LaJeunesse 2001, Santos et al. 2001, Toller et al. 2001a).

The purpose of this review is to synthesize research of the past dozen years that has used molecular DNA techniques to quantify, classify, and study the distribution of diversity in *Symbiodinium*. In his original description of *Symbiodinium microadriaticum*, Freudenthal (1962) observed "a sound taxonomy of the zooxanthellae—one taking into account pure-culture studies and host-symbiont specificities—is needed for ecological work on coral and other zooxanthellae associations."

This statement remains a valid motivation for research on *Symbiodinium* today. However, with the rise of molecular methods for identification, certain avenues of research—notably those dealing with partner specificity, biogeography, and ecology—have advanced rapidly over the past few years in ways that Freudenthal could not have anticipated. This review emphasizes how molecular techniques have been applied to studying field-collected material from diverse hosts, environments, and locations—an approach that has revolutionized our understanding of how complex and flexible these associations can be. An implicit motivation behind much of this research has been to understand the role of symbiont diversity and/or flexibility in determining possible long- and short-term responses of coral reefs to environmental change and global warming. Consequently, this review focuses principally on scleractinian coral symbioses as the principal builders of contemporary coral reefs and the subjects of most of the research undertaken during this time.

DIVERSITY, PHYLOGENY, AND SYSTEMATICS OF *SYMBIODINIUM*

Diversity

There are currently eleven named species in the exceptionally diverse genus *Symbiodinium* (Figure 1). All four formally described species (*S. microadriaticum*, *S. pilosum*, *S. kawagutii*, and *S. goreaui*) have been distinguished using the morphological species concept (Freudenthal 1962, Trench 2000, Trench & Blank 1987), and a similar rationale has been used to name an additional six species ("*S. californium*," "*S. corculorum*," "*S. meandrinae*," "*S. pulchrorum*," "*S. bermudense*," and "*S. cariborum*") without formal description, although some of these names may be synonymous (Banaszak et al. 1993, Rowan 1998). A further species ("*S. muscatinei*") has been distinguished solely from molecular sequence data (LaJeunesse & Trench 2000). In addition, the described species *Gymnodinium linucheae* (Trench & Thinh 1995) is also recognized, on molecular grounds, to be a member of the genus *Symbiodinium* (LaJeunesse 2001, Wilcox 1998), and an additional *Symbiodinium* species (closely related to "*S. californium*") has been misidentified as *Gymnodinium varians* (LaJeunesse & Trench 2000).

Lack of observed sexual reproduction in this group precludes the use of the biological species concept to define species boundaries, although various genetic measures suggest these microalgae reproduce sexually (Baillie et al. 1998, 2000b; Belda-Baillie et al. 1999; Goulet & Coffroth 1997; LaJeunesse 2001; Santos et al. 2003b; Schoenberg & Trench 1980a). In documenting diversity in *Symbiodinium*, problems recognizing distinct species have been compounded by difficulties associated with the need to culture these microalgae for morphological description. However, increasing success in recognizing diversity using molecular methods has resulted in the de facto use of the phylogenetic species concept (Eldredge & Cracraft 1980) to distinguish taxa, particularly when they also have distinct ecological or host-specific distributions. Many of the molecular types thus

identified are separated by genetic distances that are many times those found separating recognized species of free-living dinoflagellates. Consequently, a justifiable argument has been made that the genus *Symbiodinium* is speciose (Blank & Trench 1985a,b; Rowan 1998; Rowan & Powers 1992), consisting of several major clades or lineages ("subgenera") each containing multiple species. However, the use of sequence data to define species boundaries may well be confounded by the highly unusual nuclear characteristics of these dinoflagellates (e.g., Rizzo 1987) and their probably haploid nature (Santos & Coffroth 2003), making any informative conclusions premature at this stage.

Insufficient sampling also hinders our ability to determine exactly how many "species" exist within each of the principal *Symbiodinium* clades. The rate of discovery of novel molecular types continues to increase rapidly (Baker 2003) with current estimates reaching 100 or more (LaJeunesse 2001, 2002; LaJeunesse et al. 2003; T.C. LaJeunesse, unpublished data) each of which LaJeunesse (2001) considers distinct at the species level [but see S.R. Santos, T.L. Shearer, A.R. Hannes, M.A. Coffroth, submitted manuscript, for evidence of even finer subdivision, and Rodriguez-Lanetty (2003) for a quantitative estimate of lineage diversity]. At even finer taxonomic resolution, isozymes, randomly amplified polymorphic DNA (RAPDs), DNA fingerprinting, and microsatellites have reported extreme population-level variability in *Symbiodinium* (Baillie et al. 1998, 2000b; Goulet & Coffroth 1997, 2003a,b) and have demonstrated that hundreds of unique genotypes may exist for each of the taxa distinguished to date (Santos & Coffroth 2003).

Phylogeny

Molecular phylogenies of *Symbiodinium* have been dominated by the use of nuclear genes encoding ribosomal RNA (nrDNA). These studies have included the ribosomal small subunit (SSU) (Brown et al. 2002a, Carlos et al. 1999, Darius et al. 2000, Rowan & Powers 1992, Sadler et al. 1992), partial large subunit (LSU) (Baker 1999, Loh et al. 2001, Pawlowski et al. 2001, Pochon et al. 2001, Savage et al. 2002a, Toller 2001b, Van Oppen et al. 2001, Wilcox 1998), and internal transcribed spacers (ITS 1 and 2) and 5.8S regions (Brown et al. 2000, 2002; Hunter et al. 1997; LaJeunesse 2001, 2002; LaJeunesse et al. 2003; Savage et al. 2002a; Van Oppen et al. 2001). Recently, partial LSU chloroplast rDNA (cprDNA) sequences have been used to independently test the relationships inferred from nrDNA (Santos et al. 2002a,b, 2003a).

Together, these studies have recognized between four and ten distinct clades of *Symbiodinium*. Despite differences in the phylogenetic diversity of source material and semantic disagreement over which clades deserve their own name, a surprising degree of congruence between these phylogenies exists. In particular, the independent organellar marker (LSU cprDNA) used by Santos et al. (2002a) recovered a phylogeny that was not significantly different from established nrDNA phylogenies, although some uncertainty in the relative positions of clades *B*, *C*, and *F* was indicated (Baker 1999, Carlos et al. 1999, Darius et al. 2000,

LaJeunesse 2001, Loh et al. 2001, Pawlowski et al. 2001, Pochon et al. 2001, Rowan & Powers 1992, Savage et al. 2002a, Van Oppen et al. 2001, Wilcox 1998). Congruent datasets from independent nuclear and organellar sources strongly support the phylogeny presented in Figure 1, which recognizes seven distinct clades (*A* through *G*) and follows nomenclature established by Rowan & Powers (1991b), Baker (1999), Carlos et al. (1999), LaJeunesse & Trench (2000), Pochon et al. (2001), and Rodriguez-Lanetty (2003). *Symbiodinium F*, as the least well-resolved clade, would benefit from further analysis to determine the support for its highly divergent members (see Rodriguez-Lanetty 2003), including *S. kawagutii*, which earlier reports had placed in clade *C* (e.g., Banaszak et al. 2000, Carlos et al. 1999, Santos et al. 2001).

Systematics and Nomenclature

The usefulness of a name is reliably reflected by the extent to which it is employed by independent authors. In this context, the arbitrary *A*, *B*, and *C Symbiodinium* classification system introduced by Rowan & Powers (1991b) has proved remarkably useful: All molecular studies of *Symbiodinium* published to date have employed the same nomenclature to refer to the same lineages. However, recent disagreement over the expansion of Rowan & Powers' (1991b) original nomenclature to include *Symbiodinium* diversity not named by them has led to some confusion.

This confusion centers around the introduction of *Symbiodinium E* to refer to a group of symbionts found in Caribbean scleractinian corals (Toller et al. 2001a,b)—a practice followed by Goodson (2000), Brown et al. (2000, 2002a), Savage et al. (2002a), and Chen et al. (2003a,b) for corals containing similar symbionts from Thailand, St. Croix, Taiwan, and Hong Kong. Recognizing that *Symbiodinium D* had been used by Carlos et al. (1999) to refer to an unusual isolate from the interstitial water of a sponge, Toller et al. (2001a,b) distinguished newly discovered symbiont types as *Symbiodinium E*. However, sequence analysis of partial LSU sequences from both nuclear and chloroplast rDNA (Pochon et al. 2001, Santos et al. 2002a) reveal that the symbionts referred to as *Symbiodinium E* by Toller et al. (2001a,b) are distantly related members of the same clade as the *D*-type originally identified by Carlos et al. (1999), a finding supported by additional analysis (X. Pochon, unpublished data). Ironically, this lineage of symbionts was apparently documented from a Hawaiian scleractinian coral in Rowan & Powers' (1991b) original phylogeny, but it was not given a name and no sequence data were provided. Carlos et al. (1999) determined that the sponge isolate and the unusual coral symbiont of Rowan & Powers (1991b) shared a similar RFLP genotype, lending further support to the conclusion that they belong to the same clade.

While the naming of clades is wholly a question of semantics, and deciding which clades are worthy of names within an emerging phylogeny of *Symbiodinium* is a somewhat arbitrary process, names have value only if used consistently. The

recommendation made here follows the practice of Baker (1999, 2001, 2003), Glynn et al. (2001), LaJeunesse (2001, 2002), Loh et al. (2001), Pawlowski et al. (2001), Pochon et al. (2001), Van Oppen et al. (2001), Santos et al. (2002a,b; 2003a), and LaJeunesse et al. (2003), Ulstrup & Van Oppen (2003), Van Oppen (2003), in using *Symbiodinium D* to refer to the single clade that includes both the unusual sponge isolate identified as *D* by Carlos et al. (1999) and the symbionts of certain scleractinian corals originally referred to as *D* by Baker (1999) and subsequently referred to as *E* by Toller (2001a,b). *Symbiodinium E* is used to refer to the clade that includes temperate symbionts isolated from Californian *Anthopleura* named "*S. californium*," and a free-living dinoflagellate misidentified as *Gymnodinium varians* cultured from a water sample taken from Wellington, New Zealand (41°S) (LaJeunesse & Trench 2000).

How diverse are the principal clades of *Symbiodinium*, and how are taxa within these clades related to one another? The most comprehensive *Symbiodinium* phylogenies to date (Pawlowski et al. 2001, Pochon et al. 2001) have been relatively successful in using LSU nrDNA to identify variation within all *Symbiodinium* clades except *B* and *E*. However, the phylogenetic structure of this variation is not well-resolved. In particular, a large cluster of closely related *B*- and *C*-types that have also been difficult to distinguish in other nuclear SSU and LSU rDNA datasets (Baker 1999, Darius et al. 2000, Rowan & Powers 1991b, Wilcox 1998) remains unresolved in these analyses. The extreme number of sequence variants in *Symbiodinium C* led Baker (1999) and Toller et al. (2001a) to conclude that although different *C*-types did exist within this clade, much of the variation represented artifacts of cloning (Speksnijder et al. 2001) and/or paralogous genes within the rDNA repeat (Rowan & Powers 1991a,b).

More recently, sequence analysis of more rapidly evolving nuclear ITS nrDNA sequences has resolved additional phylogenetic structure within all the principal clades ("subgenera") of *Symbiodinium* (LaJeunesse 2001, 2002; LaJeunesse et al. 2003; Rodriguez-Lanetty 2003; Savage et al. 2002a; Van Oppen et al. 2001). Although one subclade of *C* still contains a number of closely related sequence variants, LaJeunesse (2001) has argued this variation, rather than being artifactual, represents rapid diversification from a single ancestral taxon (Rodriguez-Lanetty 2003; T.C. LaJeunesse, submitted manuscript). It now appears clear that significant variation, not easily distinguished by cloning-based approaches, does indeed characterize this and other clades.

Figure 1 presents a comprehensive analysis of all 294 sequences of the D1-D2 region of *Symbiodinium* LSU nrDNA (~650 nt) available in Genbank as of May 2003. Certain clades not well-resolved in Figure 1 (particularly *B*, *C*, and *D*, for which many sequences are available) comprise many distinct taxa whose phylogenetic relationships are not unequivocally resolved in this analysis. Finer resolution of distinct types within these clades has been obtained using a variety of molecular screening techniques that include restriction fragment length polymorphism (RFLP) analysis of SSU and LSU nrDNA (Baker 1999;

Baker et al. 1997; Chen et al. 2003a,b; Glynn et al. 2001; Loh et al. 1998, 2001; Pochon et al. 2001; Rowan & Powers 1991a,b, 1992; Toller et al. 2001a,b; Wilcox 1998), temperature gradient gel electrophoresis (TGGE), and denaturing gradient gel electrophoresis (DGGE) of SSU nrDNA (Belda-Baillie et al. 2002, Carlos et al. 2000), DGGE analysis of ITS and 5.8S nrDNA (Baillie et al. 2000a; LaJeunesse 2001, 2002; LaJeunesse et al. 2003), single strand conformational polymorphism (SSCP) analysis of ITS nrDNA (Ulstrup & Van Oppen 2003, Van Oppen 2003, Van Oppen et al. 2001), length heteroplasmy of LSU cprDNA (Santos et al. 2001, 2002a,b, 2003a) and phylogenetic analysis of microsatellite flanking regions (S.R. Santos, T.L. Shearer, A.R. Hannes, M.A. Coffroth, submitted manuscript). An unfortunate consequence of the variety of different molecular markers and methods used in these *Symbiodinium* surveys is that direct comparisons of different datasets are not possible. A collaborative multiple-marker study of the diverse symbiont types thus far identified would be the only way to proceed in establishing a truly comprehensive phylogeny and a consensual nomenclature.

How do genetically different *Symbiodinium* vary functionally from one another? It is clear that closely related symbiont taxa can differ significantly in their physiological capacities (e.g., Chang et al. 1983; Iglesias-Prieto & Trench 1997; Warner et al. 1996, 1999) and host specialization (Diekmann et al. 2002, LaJeunesse 2002), making generalizations regarding the properties of particular clades (particularly the diverse clades *A*, *B*, *C*, and *F*) is premature at this stage (Goodson et al. 2001, Savage et al. 2002b; but see also Knowlton & Rohwer 2003, Rowan 1998). However, as molecular advances improve our ability to distinguish more closely related types, physiological patterns not apparent in earlier molecular studies (e.g., Savage et al. 2002b) may become apparent (e.g., Santos et al. 2002a). Functional diversity of *Symbiodinium* remains an important avenue of future research whose findings remain beyond the scope of a comprehensive review now.

SPECIFICITY OF HOSTS AND SYMBIONTS

Systematic Patterns of Symbiont Distribution

An overview of the distribution of the principal clades and subclades of *Symbiodinium* reported from different host taxa is shown in Figure 1. From this distributional dataset it is clear that associations between *Symbiodinium* and its various invertebrate and protist hosts exhibit specificity (sensu Dubos & Kessler 1963): patterns of association are clearly nonrandom and the ratio of observed combinations of hosts and symbionts compared with the range of possible combinations is very small (Rowan 1991; Trench 1988, 1992). However, an emerging picture of considerable flexibility on the part of both hosts and symbionts reveals that the idea of uniformly strict specificity—in which all hosts exclusively contain

only one symbiont type—is incorrect (Trench 1988, 1992, 1993, 1996). One reason why the notion of strict specificity may have prevailed for so long is that *Symbiodinium* taxonomy from the 1950s to the early 1990s relied on the morphological study of cultured material. Culturing *Symbiodinium* reduces the diversity of heterogeneous isolates, favoring nonrepresentative members over previously dominant types (Santos et al. 2001). Early conclusions of strict symbiont specificity may therefore have been partly the result of a long-term culture that reduced the diversity of the original isolate to a single algal genotype that was mistakenly identified as "the" symbiont of a particular host species.

Scleractinian corals are among the most flexible hosts identified to date, containing symbionts from clades *A*, *B*, *C*, *D*, and *F*. However, this relative high diversity may be an artifact of sampling for these well-studied hosts. Benthic soritid foraminifera also show remarkable diversity, containing symbionts in clades *C*, *F*, and *G*. Anemones of various kinds show considerable symbiont diversity (members of clades *A*, *B*, *C*, *D*, and *E*), as do zoanthids (members of *A*, *B*, *C*, and *D*), milleporine fire corals (members of *A*, *B*, and *C*), and tridacnid clams (members of *A* and *C*). (See Figure 1.)

The relative ease with which diverse symbionts have been found in many different hosts suggests that we cannot as yet reject the null hypothesis that many (perhaps all) host taxa are able to associate with more than one type of *Symbiodinium*. Laboratory infection experiments suggest that hosts can become infected with a wide variety of different symbionts (Fitt 1984, 1985b; Schoenberg & Trench 1980c), and the fact that hosts in nature can also contain small numbers of (often unusual) minor symbionts within a generally homogeneous population of "normal" symbiont types suggests that what we perceive as specificity may be perhaps no more than the end result of competitive exclusion between symbionts (Goulet & Coffroth 1997, LaJeunesse 2002). Some of these minor types may be predominantly free-living *Symbiodinium* that are merely "moonlighting" as symbionts—they never dominate individual hosts under natural conditions but can occasionally emerge as the dominant species in culture (LaJeunesse 2002, Santos et al. 2001). We should be conservative in interpreting observed patterns of association as representing the full range of possible combinations. By implicitly recognizing specificity as a continuous variable we can distinguish which symbionts are probable (often dominant in a host) from which symbionts are only possible (rare in a host, but possibly dominant in different circumstances or different hosts). New molecular methods applied to field-collected material are paving the way for investigations of this kind (LaJeunesse 2001, 2002; LaJeunesse et al. 2003; Santos et al. 2003a; S.R. Santos, T.L. Shearer, A.R. Hannes, M.A. Coffroth, submitted manuscript). Additionally, unusual types arising in culture can fortuitously assist us in our task of recovering a comprehensive phylogeny of *Symbiodinium*. For example, Santos et al. (2003c) cultured an uncommon *Symbiodinium D* from an anemone isolate that may not be representative of its dominant populations in hospite.

Host Specificity Versus Symbiont Specificity

A new understanding arising largely from the application of molecular genetics suggests that some coral hosts are able to associate with a variety of distantly related symbiont types, while others are apparently restricted to a single symbiont type or subset of closely related types. Similarly, some algal symbionts are widely distributed and found in many hosts ("generalists"), while others appear endemic to particular locations and may be restricted to a particular host taxon ("specialists") (Rowan 1998, Baker 1999, Toller et al. 2001b, LaJeunesse 2002). We should therefore distinguish between host specificity (the specificity of hosts for a particular range of symbionts) and symbiont specificity (the specificity of symbionts for a particular range of hosts). In general, hosts appear more specific than symbionts: the mean number of combinations in which a given host is found tends to be less than the mean number of combinations in which a given symbiont is found (T.C. LaJeunesse, submitted manuscript).

A conceptual framework for coral-algal specificity is illustrated in Figure 2, in which examples (from the scleractinian corals) of all four combinations of

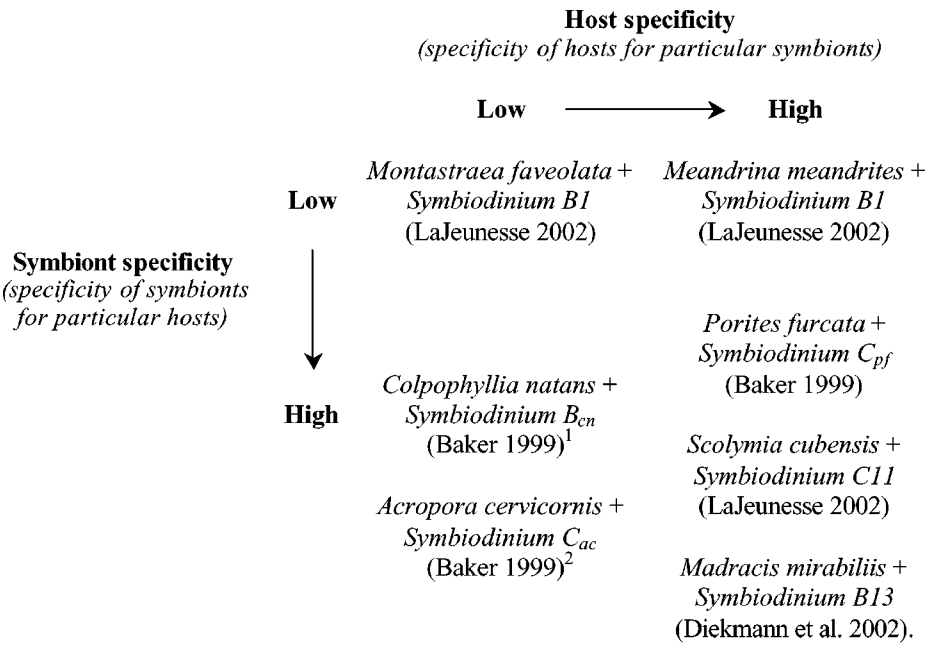

Figure 2 Conceptual framework for symbiosis specificity. Host and symbiont specificity are represented as continuous variables ranging from strict specificity to relative flexibility (low specificity). Examples of each type of symbiosis are given for *Symbiodinium* in Caribbean scleractinian corals. [1]*Symbiodinium B6* of LaJeunesse (2002). [2]*Symbiodinium C12* of LaJeunesse (2002).

low and high host and symbiont specificity are represented. One finding which emerges from classifying symbioses in this way is that a single association can be both highly flexible and highly specific, depending on which partner is being discussed. For example, the Caribbean faviid coral *Colpophyllia natans* has been found hosting (at least) one *C*-type and two *B*-types, one of which appears highly specific for *Colpophyllia* (Baker 1999, Baker & Rowan 1997, LaJeunesse 2002). This association is thus composed of a generalist host with low symbiont specificity, together with two generalist symbionts and one host-specific symbiont. The wide range of interaction strategies (Goff 1982) found in *Symbiodinium* to date supports the notion that resultant symbiosis benefits from greater evolutionary and ecological potential through flexibility.

Intraspecific Symbiont Diversity

Examples of generalist host species that are able to contain more than one symbiont type represent particularly interesting special cases. Although initially documented in Pacific *Pocillopora* (Rowan & Powers 1991a), the significance of intraspecific symbiont diversity was first recognized in later studies of Caribbean *Montastraea* (Rowan & Knowlton 1995; Rowan et al. 1997; Toller et al. 2001a,b). These studies documented four different symbiont taxa (in four distinct clades of *Symbiodinium*) in three closely related host species, and they showed that these symbionts were distributed within single host species (and even within single coral colonies) in ecologically meaningful ways (see Ecology below). Examples of scleractinian species hosting multiple symbiont taxa are now common (Baker 1999, 2001; Baker et al. 1997; Glynn et al. 2001; LaJeunesse 2001, 2002; LaJeunesse et al. 2003; Pawlowski et al. 2001; Pochon et al. 2001; Santos et al. 2001; Van Oppen 2001). Baker (1999) conservatively reported that 38 of 107 species (36%) of scleractinian corals surveyed from the Caribbean, far eastern Pacific and Great Barrier Reef (GBR) contained multiple *Symbiodinium* types, a finding that has been supported in surveys of Caribbean reef invertebrates (LaJeunesse 2002). Intraspecific symbiont diversity is not confined to the scleractinian corals: similar flexibility within single species of host has been found in foraminiferans (Pawlowski et al. 2001, Pochon et al. 2001), anemones (Santos et al. 2003c), gorgonians (Coffroth et al. 2001; Santos et al. 2003b; S.R. Santos, T.L. Shearer; A.R. Hannes; M.A. Coffroth, submitted manuscript; but see also Goulet 1999, 2003a,b) and hydrocorals (Baker 1999, LaJeunesse 2002).

Exactly how deterministic is specificity? Do unusual symbionts occasionally appear in normally highly specific hosts, or do highly specific symbionts occasionally colonize unusual hosts? Strictly specific one-on-one partnerships are difficult to document with certainty because it is impossible to survey all hosts in all possible environments. Apparent strict specificity may merely reflect an established status quo in which a stable equilibrium has been reached. Disturbance, such as environmental change, bleaching, or disease might provide a window for opportunistic partnerships to become established (Baker 2001, 2002; Rowan 1998; Toller et al.

2001b) with significant implications for the biology of the recombinant symbiosis. In fact, because exhaustive range-wide sampling of individual species has not yet been (and probably never will be) undertaken, one might argue that we cannot as yet reject the hypothesis that all host species, at one time or another and in variously stable abundance, are able to maintain symbioses with various symbiont taxa to different degrees.

ECOLOGY OF *SYMBIODINIUM*

Studies of the biology and taxonomy of *Symbiodinium* have traditionally emphasized differences among host species rather than within them (Blank & Trench 1985a, 1986; Schoenberg & Trench 1980a,b,c; Trench 1988). A few early studies speculated on the potential significance of inter- and intraspecific symbiont diversity in explaining aspects of host biology (Dustan 1982, Gladfelter 1988, Kinzie 1970, Kinzie & Chee 1979, Jokiel & Coles 1977, Jokiel & York 1982, Sandeman 1988), but the requisite molecular tools to test these speculations were not then available. Because it has only recently been recognized that intraspecific symbiont diversity is relatively common in scleractinian corals, as well as in many other associations (see Specificity above), the consensus view has traditionally underplayed symbiont diversity.

Bathymetric Distribution of *Symbiodinium*

Initial investigations of intraspecific diversity focused on Caribbean scleractinian corals, which to date have been recorded in association with members of *Symbiodinium A*, *B*, *C*, and *D*. *Montastraea annularis* and *M. faveolata*, two principal builders of Caribbean reefs, contain members of all four of these clades in a predictable pattern of depth distribution: *Symbiodinium A*-, *B*-, and *D*-types are found in shallow water (0–6 m), while *Symbiodinium C*-types are found in deeper water (3–14 m) (Rowan & Knowlton 1995, Rowan et al. 1997, Toller et al. 2001b). *D*-types were also found in extremely deep (>35 m) colonies of *M. franksi* (Toller et al. 2001b). Further survey work documented a number of Caribbean scleractinian corals showing similar patterns (Baker 1999, 2001; Baker & Rowan 1997; Baker et al. 1997; Rowan 1998; but see Billinghurst et al. 1997, Diekmann et al. 2002). A community ecology approach to surveying the distribution of *Symbiodinium* in a suite of Caribbean invertebrate hosts also found depth zonation to be an emergent property of reef-wide patterns of symbiont distribution among a variety of invertebrate hosts (LaJeunesse 2002), drawing particular attention to the shallow-water occurrence of *Symbiodinium A* and its ability to produce UV-protecting mycosporine-like amino acids (MAAs) in culture (Banaszak et al. 2000).

The identification of "high-light" and "low-light" symbionts in scleractinian corals indicates that photoadaptation (Dustan 1982, Falkowski & Dubinsky 1981, Iglesias-Prieto & Trench 1994) is not the only way that corals can respond to

changes in irradiance. Finding different symbionts in the same species of host from different habitats also provides an ecological explanation for the apparent lack of coevolution between hosts and symbionts and the failure of many coral species to pass symbionts directly to their offspring (Rowan & Knowlton 1995).

Why do corals contain multiple symbionts? Phenotypic characters of symbioses are presumably emergent properties of the genotypes of all partners involved. It therefore follows that the ability of invertebrate hosts to exist in symbiosis with several symbiont types creates a variety of combinations whose physiological abilities are likely to be much broader than those of a strict one-on-one association. Therefore, intraspecific symbiont diversity within single species of host provides invertebrate and protist hosts with the potential for dramatic phenotypic variability (Baker 1999, 2001; Baker et al. 1997; Buddemeier & Fautin 1993; Buddemeier & Smith 1999; Buddemeier et al. 1997; Douglas 2003; Kinzie 1999; Knowlton & Rohwer 2003; Rowan 1998; Rowan & Knowlton 1995; Rowan et al. 1997) challenging the conventional focus on the host as the fundamental unit of ecological diversity (Rowan & Knowlton 1995).

Baker (2001) tested the stability of depth-related patterns of zonation in the Caribbean by reciprocally transplanting corals between shallow and deep environments. He found that, after one year, patterns of symbiont distribution only reestablished themselves in upward transplants that had experienced bleaching as a result of acute exposure to high irradiance. These colonies survived well in comparison to colonies that were transplanted downwards, which did not bleach and did not change their symbionts. These data were interpreted as supporting the notion that bleaching promotes symbiont community change, which in turn can be beneficial to the coral host by allowing it to become repopulated with symbionts that are more suited to the new environment (see Climate Change below).

In general, high-light (shallow) environments are characterized by higher symbiont diversity than low-light (deep) environments, both in the Caribbean and the Pacific (Baker 1999, LaJeunesse 2002). This is most likely a consequence of environmental heterogeneity: shallow environments are more variable both in space and time than deeper environments. It remains to be seen whether additional, unusual symbionts can be found in extremely deep environments (up to 200 m, the deepest records for scleractinian corals, e.g., Zahl & McLaughlin 1959), but this may be unlikely given that extremely low-light environments can be found in shallow environments.

The relatively straightforward intercladal patterns of depth zonation found in some Caribbean scleractinian corals do not hold for their tropical Pacific counterparts (Baker & Rowan 1997; see also Rowan 1996). In tropical Pacific corals sampled to date, symbiont communities have been dominated by members of *Symbiodinium C* and *D*, with *Symbiodinium A*, *B*, and *F* being found only occasionally at higher subtropical (16–25°) or temperate (25–35°) latitudes (see Biogeography below) (Baker 1999; Baker & Rowan 1997; Darius et al. 1998, 2000; Loh et al. 1998, 2001; Rodriguez-Lanetty et al. 2001; Rowan & Powers 1991a; Van Oppen

et al. 2001; A.C. Baker, submitted manuscript). Consequently, the relatively simplistic depth patterns of symbiont distribution involving *Symbiodinium A*, *B*, and *C* do not hold true in the tropical Pacific. Instead, several tropical Pacific scleractinians exhibit patterns of depth zonation involving different symbionts within clade *C* (Baker 1999, LaJeunesse et al. 2003, Van Oppen et al. 2001). For example, nine of 23 species (39%) of *Acropora* surveyed from the northern GBR contained two types of *Symbiodinium C* that showed consistent patterns of depth distribution, with one *C*-type in shallow colonies and a second *C*-type in deeper colonies (Baker 1999). Similar findings were reported by LaJeunesse et al. (2003) in their survey of scleractinian corals from the southern GBR, which found that nine of 25 species (36%) sampled from both shallow and deep habitats, but none of the *Acropora*, contained different symbionts.

Despite some well-documented cases of depth zonation in (particularly Caribbean) scleractinian corals, the fact remains that most of the intraspecific diversity documented to date has not been satisfactorily explained by any unifying deterministic mechanism. The stochastic and labile nature of many coral-algal symbioses may inhibit complete understanding of patterns of symbiont distribution especially considering that significant time lags may damp symbiont community response to environmental change (Toller et al. 2001a). The application of molecular techniques designed to resolve more closely related symbionts (LaJeunesse 2001, 2002; Santos et al. 2003a) has led to a rapid increase in the frequency and diversity of symbionts found within single species (Baker 2003), yet at the same time it has also been recognized that specificity, even for relatively flexible corals such as Caribbean *Montastraea*, exists. Understanding the incidence and distribution of much of this diversity represents the crucial next phase of this research.

Symbiont Diversity in Individual Hosts

In addition to within-species symbiont diversity, multiple types of *Symbiodinium* within single individuals and/or colonies have been documented in a number of hosts, including scleractinian corals (Baker 1999, 2001; Baker et al. 1997; Darius et al. 1998, 2000; LaJeunesse & Trench 2000; Rowan & Knowlton 1995; Rowan & Powers 1991b; Rowan et al. 1997; Van Oppen 2001), gorgonians (Coffroth et al. 2001; Santos et al. 2001, 2003b; but see also Goulet 1999, Goulet & Coffroth 2003a,b), tridacnid clams (Baillie et al. 2000a,b; Belda-Baillie et al. 1999; Carlos et al. 2000), and other hosts (Carlos et al. 1999).

In scleractinians, colony topography can create a landscape over which symbiont communities distribute themselves according to their photic optima (Rowan et al. 1997), producing patterns of zonation that are not unlike those found with depth (Rowan & Knowlton 1995). Rowan et al. (1997) tested the stability of these patterns by toppling vertical colonies of *Montastraea annularis*. Unlike Baker (2001), the bleaching response of these toppled colonies was not recorded, but the original within-colony symbiont distributions reestablished themselves within

six months. Individual colonies can thus host dynamic communities of *Symbiodinium* that respond to changing environments. In a survey of scleractinian corals from the Caribbean, far eastern Pacific, and GBR, 25 of 38 species (66%) that contained multiple symbiont types also exhibited the same diversity at the colony level (Baker 1999). However, the fine-scale patterning of symbiont populations in Caribbean *Montastraea* in response to the external photic environment may represent an extreme example. Such flexibility and diversity at the colony level may be unusual; for example, Baker et al. (1997) found no evidence for within-colony diversity in *Acropora cervicornis*, despite clear patterns of depth zonation, and Ulstrup & Van Oppen (2003) found within-colony symbiont diversity in *A. tenuis* varied depending on which reef colonies were sampled.

Symbiodinium D in Scleractinian Corals

The distribution of (relatively low diversity) *Symbiodinium D* is unusual in many respects. Although it appears to be distributed throughout the tropics, it does not appear to be the dominant symbiont of any particular host species (Baker 1999, LaJeunesse 2002) and appears somewhat haphazard in its distribution. Baker (1999) documented *Symbiodinium D* at the transition depth between shallow *Symbiodinium A*-types and deep *C*-types in the scleractinian coral *Stephanocoenia intersepta*, and *D*-types have also been found to be dominant in extremely deep colonies of *Montastraea franksi* (Toller et al. 2001b), and in Taiwanese corals at the limit of their depth distribution (Chen et al. 2003a). This suggests that *Symbiodinium D* is favored in conditions where other symbionts are poorly suited. In a reciprocal transplant experiment, *Symbiodinium D* appeared as a novel symbiont taxon in two recovering colonies of scleractinian coral that had bleached as a result of transplantation from deep to shallow water (Baker 2001); and following a disease-related bleaching event, *Symbiodinium D* (as well as *Symbiodinium A*) was recorded in recovering colonies (Toller et al. 2001b). Glynn et al. (2001) reported that colonies of *Pocillopora* containing *Symbiodinium D* were unaffected by bleaching during the severe 1997–1998 El Niño event in the far eastern Pacific. Chen (2003a), Toller et al. (2001a), and Van Oppen et al. (2001) documented high abundance of *Symbiodinium D* in corals from inshore locations that were thought to be subject to significant terrestrial impacts. Chen (2003b) found *D*-types to be the only symbionts found in a coral characteristic of marginal habitats in Taiwan that were subject to high temperature variability. Taken together, these data indicate *Symbiodinium D* may be a weedy or opportunistic symbiont characteristic of recently stressed or marginal habitats, and/or bleached corals in the process of recovering their steady-state symbiont communities (Baker 1999, 2001; Rowan 1998; Toller 2001a; Van Oppen 2001). This may account for its unpredictable occurrence in surveys of scleractinians (and other hosts; e.g., Burnett 2002) and suggests that the abundance of *Symbiodinium D* might reflect coral community health by providing a useful signal of recent and/or recurrent stress events.

Free-Living *Symbiodinium*

Several studies have identified apparently free-living *Symbiodinium* in the waters or sediments surrounding potential invertebrate hosts (Carlos et al. 1999, Loeblich & Sherley 1979, Taylor 1983). However, to date no studies have systematically investigated the diversity of free-living *Symbiodinium* in the environment. The only relatively unambiguous records that are accompanied by reliable molecular identifications are members of *Symbiodinium E* misidentified as *Gymnodinium varians* (LaJeunesse 2001, Rowan & Powers 1992, Saldarriaga et al. 2001, Saunders et al. 1997, Wilcox 1998) and a *Symbiodinium* in clade *A* that was isolated and cultured from the interstitial waters of Hawaiian sands (Carlos et al. 1999). An unusual and highly divergent member of *Symbiodinium D* cultured from the interstitial water of a Palauan sponge may also represent a free-living type (Carlos et al. 1999). LaJeunesse (2002) sampled *Symbiodinium* from the digestive gland and the digestive tract of the queen conch *Strombus gigas* in Mexico and found members of both *Symbiodinium B* and *C* in the tract, but only the *C*-type in the gland, suggesting that the *B*-type represented a recent ingestion of a free-living symbiont.

Adult anemones have been shown to exchange symbionts with the environment (Kinzie et al. 2001), and tridacnid clams inoculated with cultured symbionts have also been successful in establishing new symbioses (Belda-Baillie et al. 1999, Fitt 1984). Because symbionts may be attracted to vacant symbiotic hosts (Fitt 1985a), our chances of detecting unusual free-living *Symbiodinium* as surface contaminants may be greater than might be otherwise expected; despite this, however, it is likely that an extraordinary diversity of free-living *Symbiodinium* remains to be identified.

BIOGEOGRAPHY OF *SYMBIODINIUM*

Latitudinal Variation in Coral-Algal Symbiosis

Symbiont distributions in scleractinian corals vary in different parts of the world (Baker & Rowan 1997, Rowan 1996). Some symbiont taxa are widely distributed, both among different hosts and across geographic regions (Burnett 2002, Loh et al. 2001, Rodriguez-Lanetty & Hoegh-Guldberg 2003), whereas other taxa show high host specificity or appear regionally endemic (Baillie et al. 2000b; Baker 1999; LaJeunesse 2001, 2002; LaJeunesse et al. 2003; Santos et al. 2003b,c).

Community-level surveys of *Symbiodinium* in scleractinian corals have shown that members of *Symbiodinium A*, *B*, and/or *F* are more common at higher latitudes worldwide, with *Symbiodinium C* more abundant in tropical latitudes (Baker 1999, Rodriguez-Lanetty et al. 2002, Savage et al. 2002a; see A.C. Baker, submitted manuscript) (Figure 3). This pattern is true for both the Caribbean and the Pacific, despite the fact that *Symbiodinium A* and *B* are far more prevalent in tropical Caribbean corals than their Pacific counterparts (see Unusual Symbioses, below). Corals from the relatively isolated and high latitude Hawaiian archipelago have

been documented to contain members of *Symbiodinium C* and *D* and possibly also *F* [*S. kawagutii* in *Montipora verrucosa* (now *M. capitata*), although this may be an artifact of culturing] (LaJeunesse 2001; Rowan & Powers 1991a; T.C. LaJeunesse, unpublished data). Based on the patterns presented here, future surveys of the Hawaiian archipelago (20°–29°N) seem likely to uncover further diversity in additional clades such as *Symbiodinium A*.

Latitudinal differences in the distribution of *Symbiodinium* have been harder to document at the level of individual host species than at the level of the reef community. The temperate anemone *Anthopleura elegantissima* hosts two species of *Symbiodinium* that vary their distribution along the Pacific coast of North America, with northern populations (43.5°–48.5°N) containing only *Symbiodinium* in clade *B* (sometimes in combination with a *Chlorella*-like green alga), and southern populations (33°–36°N) hosting mixtures of *Symbiodinium B* and *E* (LaJeunesse & Trench 2000). In the scleractinian corals, intraspecific surveys of *Plesiastrea versipora* (Baker 1999, Rodriguez-Lanetty et al. 2001), *Seriatopora hystrix*, and *Acropora longicyathus* (Loh et al. 2001) indicate that members of *Symbiodinium C* are common in tropical populations (with *S. hystrix* being dominated by *Symbiodinium D* at equatorial locations), but members of *Symbiodinium B* (*P. versipora*) or *A* (*A. longicyathus*) become more common at higher latitudes (23°–35°S). Some evidence of geographic variation within clade *C* was also reported (Loh et al. 2001). Taken together, these reports suggest that both temperature and light have important roles to play in determining *Symbiodinium* distribution (see review in A.C. Baker, submitted manuscript).

Unusual Symbioses in the Tropical Western Atlantic

Despite broad latitudinal patterns in the distribution of *Symbiodinium* worldwide, it is apparent that scleractinian corals in the tropical western Atlantic still host *Symbiodinium A* and *B* much more commonly than their Pacific counterparts at comparable latitudes. Why should coral-algal symbioses in the Caribbean more closely resemble those found at higher latitudes in the Pacific? Increased extinction rates and faunal turnover of Caribbean scleractinian corals that coincided with the Plio-Pleistocene onset of Northern Hemisphere glaciation (Budd 2000) may have selected for symbioses those that were suited not only to cooler temperatures (Stanley 1986), but more specifically to considerably higher seasonality (Jackson et al. 1993). Conditions in the tropical western Atlantic during this time may therefore have resembled those characterizing higher latitudes, resulting in a shift to symbiont communities involving clades *A* and *B* (Baker & Rowan 1997; LaJeunesse et al. 2003; A.C. Baker, C.J. Starger, T.R. McClanahan, P.W. Glynn, submitted manuscript). These symbionts have since diversified in the endemic Caribbean scleractinian coral fauna (T.C. LaJeunesse, submitted manuscript). Pulses of cooler water in tropical environments in the western Atlantic may thus have favored the evolution of an endemic Caribbean coral fauna whose symbioses were more characteristic of those found at higher latitudes (A.C. Baker, submitted manuscipt).

Large-scale symbiont community shifts, similar to those hypothesized for Caribbean corals, may also characterize contemporary reef corals experiencing rising sea surface temperatures and recurrent episodes of mass bleaching (A.C. Baker, C.J. Starger, T.R. McClanahan, P.W. Glynn, submitted manuscript.) The high incidence of *Symbiodinium D* in scleractinian corals from tropical locations (Baker 1999; LaJeunesse et al. 2003; Loh et al. 2001; Toller et al. 2001a,b; Van Oppen et al. 2001; A.C. Baker, submitted manuscript), recently bleached reefs (Glynn et al. 2001), and extreme high temperature environments (Baker et al. 2003), together with its absence from high latitude locations sampled to date (A.C. Baker, submitted manuscript; Baker 1999; Loh et al. 2001; Rodriguez-Lanetty et al. 2001; Savage et al. 2002) support the idea that symbiont community change may already be occurring in these affected ecosystems (see Climate Change below).

FLEXIBILITY OF INDIVIDUAL HOSTS

Controversy over the role of symbiont diversity in enabling hosts to mitigate environmental change revolves largely around how quickly symbiont change within individual hosts can occur. This has been investigated by experimental manipulation (e.g., Baker 2001, Kinzie et al. 2001, Rowan et al. 1997) and by field observations of individuals in response to bleaching (see Climate Change below), disease (Toller et al. 2001a), ontogeny, and seasonality.

Host Reproduction and Ontogeny

Scleractinian corals that do not supply their offspring with symbionts must perforce re-establish their symbioses with free-living *Symbiodinium*. The pool of symbionts upon which these "open" systems rely may be dependent on the diversity of potential symbionts found in other (non-scleractinian) hosts (e.g., Lee et al. 1995). The extent to which this is true may depend largely on the particular symbionts and hosts concerned, since it is clear that some symbiont types are found in a variety of taxonomically dissimilar hosts, but that others are highly specific (LaJeunesse 2002). For example, *Maristentor dinoferus*, a giant heterotrich ciliate recently discovered in Guam contains *Symbiodinium* that are indistinguishable (by lsrDNA analysis) from those found in many scleractinian corals (Lobban et al. 2002).

Corals that maternally transfer symbionts to their offspring might be expected to contain less diverse symbionts than corals whose larvae or juveniles are required to obtain them environmentally (Douglas 1998). Despite this logical expectation, little evidence for such patterns has been observed to date (Hidaka & Hirose 2000; Van Oppen 2003). This may reflect lack of reliable information on symbiont transmission for many coral species or may indicate that many corals are able to obtain symbionts from the environment throughout their life cycle (see Goulet & Coffroth 2003a,b).

Symbiont specificity during early ontogeny is a characteristic feature of invertebrate-algal symbiosis that has been well studied in anemones (Fitt 1984,

Kinzie & Chee 1979, Schoenberg & Trench 1980c), jellyfish (Colley & Trench 1983), gorgonians (Coffroth et al. 2001, Kinzie 1974), giant clams (Fitt 1985b), and scleractinians (Schwarz et al. 1999, Van Oppen 2001, Weis et al. 2001). Most of these studies investigated host specificity for cultured or freshly isolated symbionts from the same (homologous) or different (heterologous) host species, and only recently have field investigations using molecular methods been employed to survey the natural occurrence of symbionts in larval or juvenile hosts. In a field study of a Caribbean gorgonian, newly settled polyps initially acquired diverse symbionts whose identity appeared to depend on the settlement habitat; symbiont populations reverted to the original (maternal) populations after three to six months (Coffroth et al. 2001). Similar molecular comparisons of a second gorgonian found that newly settled polyps contained different symbiont communities than adult colonies (Santos et al. 2003a).

Studies of scleractinian corals have also demonstrated the capacity for diverse symbionts to be acquired during early ontogeny (Schwarz et al. 1999, Van Oppen 2001), but some symbionts may still be favored over others (Weis et al. 2001). These findings indicate that the early ontogeny of cnidarian hosts may allow more flexible associations than the later adult stage, but it is not yet clear to what extent this flexibility can be interpreted as an ecological strategy allowing juveniles to colonize new habitats, or whether it simply represents the early proliferation of unusual symbionts in vacant hosts before a steady symbiotic state is established. Such a phenomenon may also explain the novel symbionts that appear early in the recovery of severely bleached scleractinian colonies (Baker 2001, Toller et al. 2001a).

Adult hosts may also be able to exchange symbionts with the environment in varying degrees. This has been demonstrated in anemones (Kinzie et al. 2001), but to date there is little direct evidence for this in scleractinian corals, which are not easily rendered aposymbiotic (see review in Buddemeier et al. 2003).

Seasonal Changes in Symbiont Communities

Seasonal variation, especially at high latitudes, may also create environmental variation that favors different symbiont communities. Such changes may occur in benthic foraminifera (X. Pochon, unpublished data). Community surveys of one species of scleractinian coral in southern Taiwan documented a change in relative abundance of *Symbiodinium C* and *D* on a seasonal basis, being more dominated by *D*-types in the summer compared with winter (Yang et al. 2000). While predictable seasonal change has not been documented in individual hosts (e.g., Belda-Baillie et al. 2000), corals at high latitudes in variable environments may experience shifts between symbiont populations (Thornhill et al. 2003).

CORAL REEF BLEACHING AND CLIMATE CHANGE

Principal motivations for research into *Symbiodinium* diversity, biogeography, and ecology in coral reefs are the obligate nature of these symbionts for many of their hosts (including all tropical reef corals) and the central role they play in

understanding coral reef bleaching events. Increasingly frequent and severe episodes of mass coral bleaching and mortality over the past two decades as a result of warmer baseline temperatures and increasingly severe temperature anomalies such as El Niño (Brown 1997, Glynn 1993) suggest that reef ecosystems may be fast approaching a critical survival threshold (Hoegh-Guldberg 1999). To what degree does symbiont diversity explain the inherent spatial and systematic variability in coral bleaching, and to what degree will symbiont community change and/or recombination affect future bleaching scenarios?

Variability in Coral Bleaching

Recent reviews (Baker 2003, Buddemeier et al. 2003, Knowlton & Rohwer 2003) have emphasized the importance of coral bleaching in motivating contemporary research on the diversity of *Symbiodinium*. However, understanding how symbiont diversity affects the incidence and severity of bleaching has been difficult because we usually have little knowledge of how symbionts are distributed prior to bleaching events (but see Glynn et al. 2001; Rowan et al. 1997; A.C. Baker, C.J. Starger, T.R. McClanahan, P.W. Glynn, submitted manuscript). The possibility that symbiont taxa vary in their temperature sensitivities (and hence susceptibility to bleaching) was initially proposed in the absence of any supporting evidence (Buddemeier & Fautin 1993, Gladfelter 1988, Rowan & Powers 1991a, Sandeman 1988; but see Iglesias-Prieto et al. 1992). However, this hypothesis has since been confirmed in at least two studies of scleractinian coral: Rowan et al. (1997) demonstrated that loss of members of *Symbiodinium C* at the upper limits of their irradiance distribution explained otherwise enigmatic variability in bleaching of Caribbean *Montastraea* in 1995, whereas Glynn et al. (2001) showed that patchy bleaching in Pacific *Pocillopora* was explained by the preferential loss of *Symbiodinium C*-types and retention of *Symbiodinium D*-types. Bleaching severity may also correlate with symbiont diversity in affected hosts (Baker & Rowan 1997, LaJeunesse et al. 2003, Loh et al. 2000), but the resolution of these correlations will tend to be much lower than for direct comparisons in which specific symbiont identities are known. However, despite these uncertainties, differences in bleaching susceptibility among different symbiont taxa have clear implications for how symbiont distributions might be applied to predicting or understanding future bleaching incidence and severity (Baker 2003).

Changes in Symbiont Community Structure Following Bleaching

Changes in symbiont community structure following mass bleaching events can arise in three ways that are not mutually independent: (*a*) differential mortality of bleaching-susceptible combinations (true "Darwinian" adaptation, or natural selection); (*b*) quantitative change in the relative abundance of existing symbiont communities within colonies (symbiont "shuffling"); and (*c*) qualitative change by recombination with symbionts acquired from the environment (symbiont "switching"). The first process follows logically from mass mortality of bleached corals

containing bleaching-susceptible symbionts (see Variability above). The latter two processes form part of the "adaptive bleaching hypothesis" (ABH) proposed by Buddemeier & Fautin (1993). Some confusion has arisen over the misunderstanding that the ABH applies exclusively to symbiont "switching" involving exogenous pools of prospective symbionts (Hoegh-Guldberg 1999, Hoegh-Guldberg et al. 2002); this is not the case (Baker 2002, Buddemeier et al. 2003).

Much of the controversy surrounding the ABH centers around how quickly different and/or novel symbiont communities can become established in individual hosts during a bleaching event and whether the "ecospecies" (Buddemeier et al. 2003) thus created is more likely to survive as a result (Douglas 2003, Hoegh-Guldberg 1999). Extensive mass mortality of reef corals following bleaching is used as de facto evidence against the hypothesis, and the lack of any evidence for partner recombination following natural episodes of bleaching (Hoegh-Guldberg et al. 2002) is also seen as evidence against the idea. However, few attempts to monitor symbiont communities during bleaching have been undertaken to date (Baker 2002), and the results of these studies have tended to support, rather than refute, the basic ideas of the ABH (Baker 2001, Glynn et al. 2001, Rowan et al. 1997, Toller et al. 2001a). The capacity of reef corals to become dominated by different symbionts following dramatic environmental change and bleaching has been documented in field experiments (Baker 2001, Rowan et al. 1997), and changes in symbionts can still occur (although these displacements may be only transitory) even when environmental conditions return to normal after bleaching (Toller et al. 2001a, see also Thornhill et al. 2003). However, none of these experiments have been able to distinguished quantitative change (in endogenous symbiont communities found within individual colonies) from qualitative change (involving exogenous populations of symbionts from the environment).

Recent studies indicate that bleaching does not represent the sudden breakdown of an otherwise stable relationship in which symbiont standing stocks are held constant. Instead, bleaching is an extreme version of a symbiont regulatory mechanism in which algal densities change in response to a changing environment (Fagoonee et al. 1999, Fitt et al. 2000, Kinzie 1999) over seasonal (and shorter) timescales. Symbiont community change by switching (an "open" symbiotic system) or shuffling (a "closed" symbiotic system) may occur without visible bleaching; severe bleaching may merely accelerate this process by promoting turnover of existing partnerships (Baker 2001, Buddemeier & Fautin 1993).

The Future of Coral Reefs

The extent to which symbiont diversity and flexibility will affect the long-term future of coral reefs in response to continued climate change is not yet clear. Although evidence exists indicating that diverse symbionts can significantly buffer the effects of climate change (by differential mortality of bleaching-susceptible combinations and/or symbiont switching or shuffling within hosts), the scales

over which such mechanisms might occur are as yet unknown and many important questions remain. What fraction of existing symbioses on coral reefs might be considered bleaching susceptible, and to what degree does symbiont community structure on reefs remain constant over time? How long might it take for bleached reefs to recover from (the perhaps few) bleaching-resistant symbioses that survive, and might we nevertheless suffer irreversible ecological phase shifts as a result of significant coral loss (Done 1999, Hoegh-Guldberg 1999, Knowlton 1992)? Can we still expect ecological extinction of reefs in some areas, despite the longer-term persistence of coral reefs worldwide (Buddemeier & Smith 1999, Buddemeier et al. 1997, Smith & Buddemeier 1992)? How often do bleached individuals recover with quantitatively different (shuffled) or qualitatively different (switched) symbiont communities, and does bleaching accelerate either of these processes (Baker 2001, Buddemeier & Fautin 1993)? These are the underlying questions that must be addressed in order to establish the degree to which symbiont community change on reefs is possible over ecological (as opposed to evolutionary) timescales and whether or not individual colonies are able to modify their symbiont communities rapidly enough to adapt or acclimatize to a changing local climate.

The spatial resilience of coral reefs—the dynamic capacity of a reef to avoid thresholds at a regional scale (Nystrom & Folke 2001, Nystrom et al. 2000)—may be significantly increased by the diverse and flexible nature of symbioses involving *Symbiodinium*. Human efforts to increase the spatial resilience of coral reefs to bleaching through the creation and management of Marine Protected Area (MPA) networks (West & Salm 2003) should explicitly incorporate unusual and diverse habitats that maximize symbiont diversity into their design. When coral reef hosts are assessed over their full range of systematic, ontogenetic, ecological, and biogeographic gradients, the existence of unusual symbionts normally found only in uncommon host taxa, larval stages, marginal environments, or at latitudinal extremes may prove critical in understanding the long-term resilience of coral reef ecosystems to environmental perturbation.

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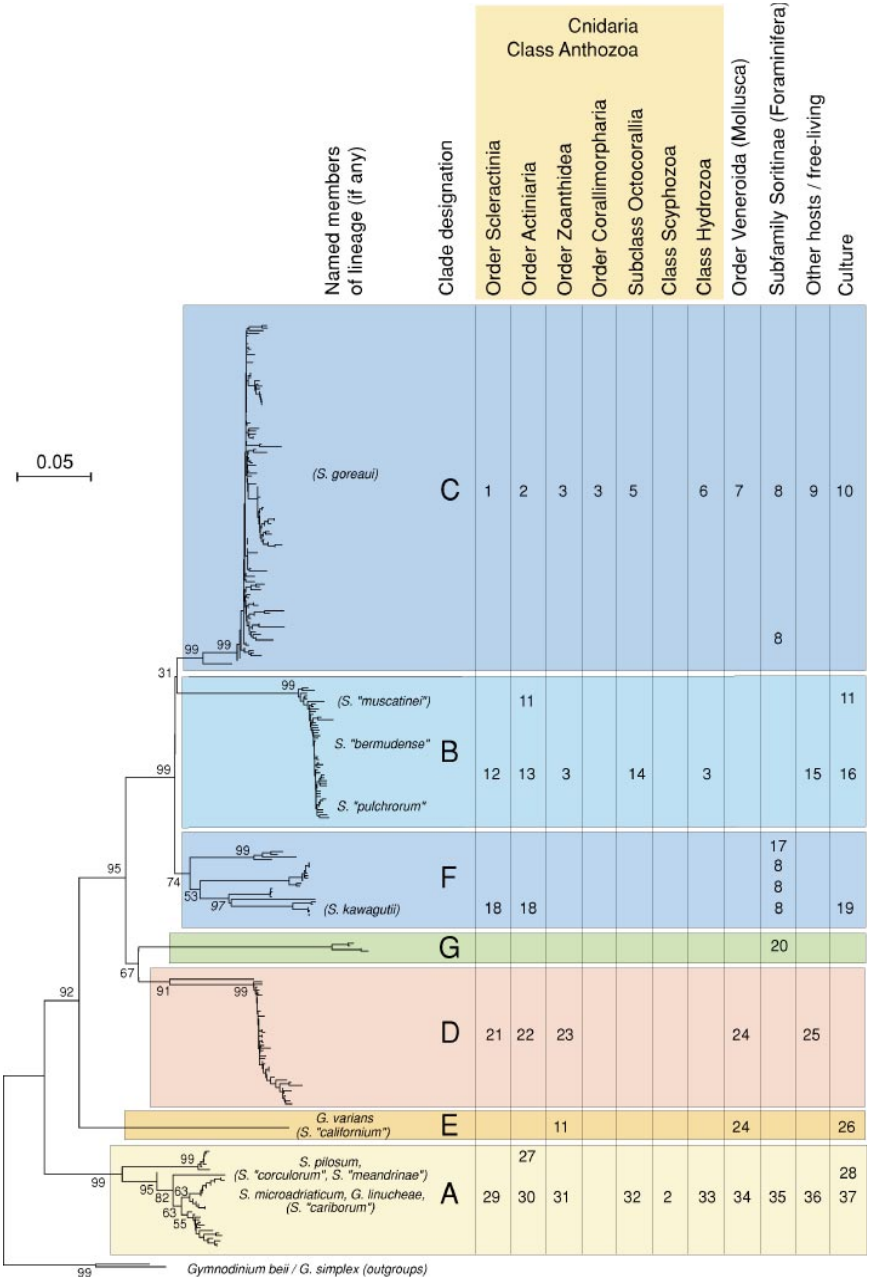

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Figure 1 Molecular phylogeny of *Symbiodinium* indicating seven principal clades *A–G* (*left*), the eleven named species (*center*), and the distribution of the principal clades (and subclades) of *Symbiodinium* among different host taxa (*right*). LSU nrDNA sequences (~600 nt) were aligned using Clustal X (Thompson et al. 1997) and phylogenetic analyses performed by neighbor-joining using PAUP 4.0 (Swofford 2002). Reliability of internal branches was assessed by 1000 bootstrap replicate analyses (numerical values shown at nodes). Scale bar represents number of substitutions per site. Position of named species in parentheses is included for illustrative purposes only; LSU rDNA sequence data not available for these taxa. Identifications based on cultured material are excluded for the purposes of host distribution. Details on phylogenetic reconstruction, Genbank Accession numbers, and literature references represented by numerals in right-hand columns can be found in our website supplementary materials (Follow the Supplemental Materials link from the Annual Reviews home page at http://www.annualreviews.org).

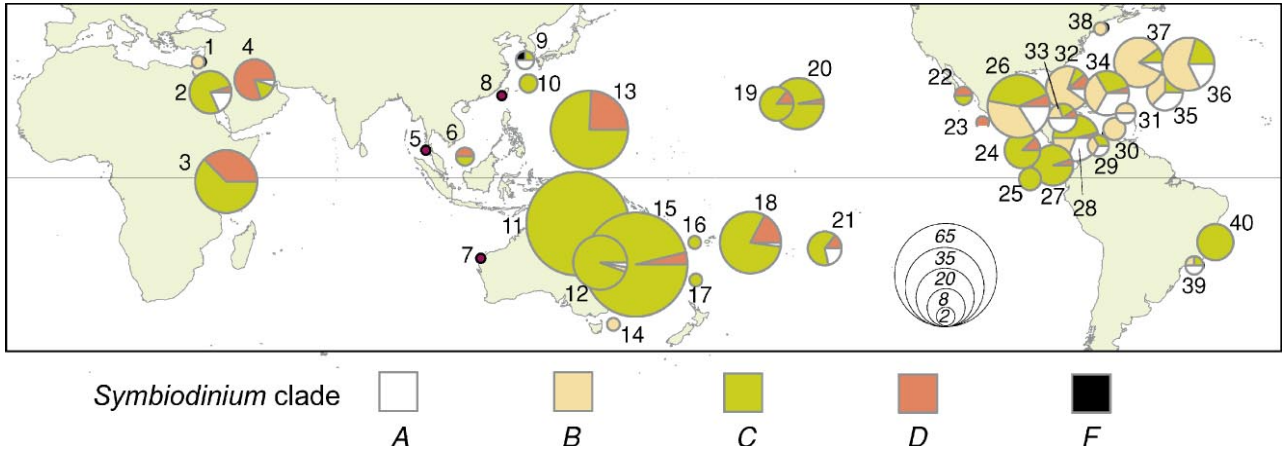

Figure 3 Global distribution of Symbiodinium in shallow water scleractinian corals (<5–7 m). Pie charts reflect distribution of different clades A, B, C, D, and F among species of coral host sampled, with the diameter of the pie chart approximately proportional to the square root of the number of species sampled (see inset scale). Numerals next to pie charts refer to data source listed in Table 2 (Follow the Supplemental Materials link from the Annual Reviews home page at http://www.annual-reviews.org)). Modified from A.C. Baker (submitted manuscript).

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