

## WHO ARE THE PLAYERS ON CORAL REEFS AND DOES IT MATTER? THE IMPORTANCE OF CORAL TAXONOMY FOR CORAL REEF MANAGEMENT

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Coral reefs are the most diverse communities in the sea, probably with 1–9 million species, most of which are undescribed (Reaka-Kudla, 1997). The corals themselves, however, represent only a small portion of this diversity, and discoveries of new species are fairly rare. For example, only a few new (or newly resurrected) reef-building scleractinian species have been formally described in the neotropics over the last decade (Zlatarski, 1990; Weil and Knowlton, 1994; Budd and Guzman, 1994). This state of affairs might lead one to assume that current taxonomic understanding of corals is largely complete and thus adequate for effective coral reef management. Rather, I would argue that these recent discoveries represent the tip of an iceberg of unknown size, and moreover, that taxonomic uncertainty and ignorance hinders our ability to manage and protect reefs in several important ways.

One source of taxonomic uncertainty stems from the debate over the nature of species boundaries in corals. At one end of the spectrum is the view that coral species are broad and fuzzy entities, capable of interbreeding with distantly related forms and exhibiting wide morphological variability and large ecological and geographical ranges (e.g., Veron, 1995). At the other end of the spectrum is the view that corals are well defined reproductively and are more narrowly distributed and less variable than conventionally assumed (e.g., Knowlton and Jackson, 1994). This argument persists in part because phenotypic plasticity (Bruno and Edmunds, 1997) and slow rates of molecular evolution (Romano and Palumbi, 1997; Van Oppen et al., 1999; Medina et al., 1999) make it technically difficult to identify the phenotypic or genotypic correlates of reproductive boundaries.

A second source of taxonomic uncertainty has to do with zooxanthellae. Coral systematists could ignore these symbiotic dinoflagellates when conventional wisdom indicated that all corals hosted the same type of symbiont. This is now clearly not the case; variation among symbionts exists not only among different host species, but also within host species and even single colonies (Rowan, 1998). Consequently, corals as ecological entities are defined not only by the coral animal genotype, but also by the genotype or genotypes of the algae that they host. Our understanding of zooxanthella diversity has increased enormously over the last decade, but it remains the case that taxonomic resolution is very coarse (at the level of family or order), based on measures of genetic diversity observed in free-living dinoflagellates (Rowan, 1998).

The history of studies of *Montastraea* provides a compelling case for the extent to which ecological understanding depends on sound taxonomy of corals and their symbionts. *Montastraea annularis* sensu lato has been the dominant reef-builder of the Caribbean for the last several million years, and it has consequently been widely studied by both biologists and geologists. For decades, extensive morphological and physiological variation across its wide depth and habitat range was attributed to phenotypic plasticity in both the coral and its symbiotic algae (Graus and Macintyre, 1976; Wethey and Porter, 1976). This (and similar assessments for other taxa) allowed Connell (1978) to argue that most corals had wide depth ranges and generally broad ecological requirements. We now know, however, that *M. annularis*

sensu lato consists of at least three species (Weil and Knowlton, 1994); these taxa can be distinguished by clear genetic differences in some cases (Lopez et al., 1999), and evidence for reproductive barriers involving either fertilization or timing of spawning is also emerging (Knowlton et al., 1997; Levitan and Knowlton, in prep.). Moreover, each of these coral species is capable of hosting one or more of four major groups of zooxanthella, resulting in a minimum of 12 ecologically distinct entities (Rowan, 1998; Toller et al., in prep.). Thus the quintessential generalist has become, with better taxonomic understanding, a complex of far more specialized forms. At present it is impossible to say how many other coral 'species' are in fact species complexes, because the literature reports numerous forms or morphotypes (e.g., Fenner, 1999) that remain to be analyzed. Similarly, the distributions of zooxanthellae in these other corals are less well documented, and the ecological significance of variation within major groups of zooxanthellae is essentially unknown for any coral (Rowan, 1998).

Despite this uncertainty, skeptics might argue that our current level of taxonomic resolution, coarse though it might be, is adequate for many aspects of coral reef management. Indeed, why not use a functional group approach (Steneck and Dethier, 1994), e.g., branching corals, massive corals, etc., and ignore most aspects of taxonomy altogether? Although such ecologically based groupings can be adequate for many purposes, they are likely to get us in trouble in other areas.

One of the clearest cases where taxonomy and ecology meet is in coral reproduction. Entities that do not interbreed are distinct species using essentially any species concept (Knowlton and Weigt, 1997), and we need to know what those entities are. This is particularly true for the many important reef-building corals that engage in mass spawning. Such species rarely self (Carlon, in press), so that fertilization depends on the ability of sperm from one colony to find eggs from another conspecific colony. The chances of this happening drop as sperm become more dilute and older, so that there must exist a critical threshold density below which sexual reproduction no longer reliably succeeds (Levitan, 1998). We cannot estimate such a density unless we know which individuals are capable of interbreeding.

Reef restoration projects also depend on good taxonomy. Care must be taken to ensure that transplanted colonies (including their symbionts) are placed in areas to which they are well suited. Many corals exhibit variation across depth in the symbionts they host (Rowan, 1998), and thus sources of transplanted material should be chosen with this in mind. Although corals may be able to survive under ideal circumstances with suboptimal symbionts, rates of partial mortality from predators, competitors, disease, or physical disturbance may exceed new growth when the match between symbionts and habitat is poor, resulting in eventual death. The comparatively high cost of restoration projects makes such careful taxonomic evaluation of special importance.

Choice of regions meriting special protection on the basis of endemic faunas also depends on sound taxonomy. We have traditionally assumed that most coral species are very widespread, but little data exist to support this assumption. In the tropical Atlantic for example, differences between northern and southern representatives of the *M. annularis* complex have been noted (Weil and Knowlton, 1994), but their taxonomic significance remains unresolved. The issue of geographic variation also leads to the related question of population structure. Given the difficulty of recognizing species, it should come as no surprise that we know essentially nothing about the boundaries of populations. Progress on both fronts will depend on the development of genetic markers that are effective at relatively fine levels of differentiation. Regional systems of reefs may function as

metapopulations (Mumby, 1999), but the relevant parameters for understanding how such systems can persist will depend on delimiting the extent of routine and occasional dispersal events.

In conclusion, sound taxonomy underpins sound ecological management. This does not mean that management must wait until taxonomic understanding is complete, as that would be environmental lunacy. However, failure to address these taxonomic issues based on the argument that we already know what we need to know would be equally short-sighted.

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