

**Sex, Symbiosis and Coral Reef Communities.** ROBERT A. KINZIE III.  
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## **Sex, Symbiosis and Coral Reef Communities**

### **Abstract:**

Questions about how today's corals and coral reefs will fare in a future that holds not only increasing direct anthropogenic impacts, but also global change, cannot be satisfactorily answered if we do not understand the relations of corals and reef systems to today's environmental conditions. This paper discusses four aspects of modern reef biology: coral reproduction, coral population biology, the coral-zooxanthella symbiosis, and reef community ecology. Conclusions of this survey of current knowledge are that complexities of cnidarian reproductive biology, and our rudimentary knowledge of reproductive patterns in reef cnidarians, make forecasting based on current knowledge uncertain at best; new discoveries about the coral algal symbiotic system suggest a possible mode of adjustment to environmental change that warrants a strong research effort; coral communities of the future may well be unlike what we are familiar with today; and these new assemblages will be shaped by the interaction of novel environmental conditions and the characteristics of individual reef species.

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Il faut se preparer a tout dans des cas si extraordinaires ... (A. Trembley in Dawson 1987)

The papers in this issue address two questions which are central to the concerns set out by Buddemeier and Smith (1998) in the introduction.

a) How much of what we have learned about living corals and extant coral reef systems reflects adjustment to the conditions of global marine climates of the past?

b) Given existing or potential models of global climate change, what future trends for corals and reefs might we predict, and how well can we

do it?

This paper gives a general overview of selected aspects of coral biology, to serve as a review for non-specialists and a prod to specialists to avoid too narrow a scope in considerations of what questions may be important, what are accepted definitions, and what aspects of coral reef science might provide needed answers to multi-scale questions about a changing world (Buddemeier and Kinzie, 1997).

The tone of this paper is intentionally speculative and prescriptive, tying together the more typical review and research papers in this issue, and pointing out aspects of coral biology that might most profitably repay new research efforts. The topics will address aspects of four facets of modern reef biology: coral reproductive and population (in its widest sense) biology--together the "sex" of the title, with emphasis on the individual and population levels; the coral-zooxanthella symbiosis, emphasizing the plasticity of the system; and reef community ecology from the traditional species composition viewpoint and from a more holistic perspective, emphasizing a process oriented approach. At the end of each of the sections I suggest topics that might be worthwhile avenues of future research.

### Coral reproduction

Reproduction in cnidarian reef builders has received a great deal of study, and while we are probably not yet at the stage where we can make many generalizations, we can certainly make one--generalizations about coral reproduction are, at this time, premature. Fautin (1997) has pointed out that in studying reproductive patterns in the structurally simple and morphologically plastic cnidarians, one must be prepared for anything, as noted by Trembly in the epigraph of this paper. In these animals there is a continuum of the processes of increase from simple mitosis (i.e., growth at the level of the polyp) to the production of reef-wide populations of ramets (i.e., growth at the level of the genotype). It is important not to forget the continuous spectra of scales--spatial, temporal and genetic--when dealing with coral reproduction (Lasker and Coffroth, 1999).

Harrison and Wallace (1990) produced a scheme wherein corals are classed as hermaphroditic or gonochoric, and as broadcast spawners or

brooders. Superimposed on this simple 2 by 2 scheme is a complex array of developmental pathways by which these animals grow, disperse and settle. Fautin's (1991) survey of development in cnidarians concludes that the "simple" structure of these diploblastic animals, which apparently places few mechanical, cytological or morphological constraints, has produced many different developmental modes with no clear patterns, either phylogenetic or ecological. Until we understand the variety of pathways and appreciate the scale of the sequellae--both spatial and temporal--we will be hampered in our ability to predict how any species might respond to environmental change.

Two factors conspire to limit projections of differential responses of corals to environmental change back into the fossil record. The first is that until recently, most coral paleontology was limited to the genus level at best, and often only to the level of family (Veron, 1995). We are learning from study of living corals that what we had thought of as distinct taxonomic units are not always well defined. Studies of characters that do not fossilize such as proteins and nucleic acids (Ayre et al., 1991; Knowlton et al., 1992; Stobart and Benzie, 1994), reproductive biology (Van Moorsel, 1983; Babcock, 1984; Harrison, 1985; Kojis, 1986; Knowlton et al., 1997), and behavior (Lang, 1971) have revealed complexity where traditional methods suggested simplicity. This uncertainty clouds our concept of what the actual adaptive units might be (Lasker and Coffroth, 1999). When features of reproductive mode and sexuality are incorporated into analyses of past events, our incomplete knowledge of what is true for living species further obscures our ability to envision the past.

Nonetheless, it is worthwhile to point out some features of reproductive biology that could be used to address the potential of corals to respond to environmental change. In discussions of the fate of coral reefs confronted by rising sea level, outcomes have been described as: "keep up," "catch up," or "give up," with the proportion of reefs falling into the last category increasing with increasing rates of sea level rise (Neumann and Macintyre, 1985). This concept is particularly pertinent to models of global change that predict a rapid rise in sea level. The question of reef response to rising sea levels is often posed by geologists, therefore potential answers are framed in terms more related to total carbonate

accretion than the biological features of reefs (Smith, 1983; Davies, 1983). Nevertheless, the ability of essentially all reef cnidarians, including framework builders, and the array of scleractinian and non-scleractinian reef organisms to produce free swimming planulae, spores, or dispersing larval stages, means that no matter how quickly sea level might rise, propagules of the species could keep pace and settle at suitable depths each generation. Such "jump up" reefs while possibly lacking in massive carbonate accumulation, might well contain most of the species present in the original community. The components of reef systems would be retained, albeit in configurations and with interspecific associations unfamiliar to us now (Buddemeier, 1992).

Another feature of coral reproductive biology showing a relationship with some, as yet undetermined, environmental factor or factors is the timing of reproduction. For example, interspecific synchrony of spawning seems to be weaker at lower latitudes (Richmond and Hunter, 1990; Kenyon, 1995). Intraspecific patterns also show geographical differences in seasonality. Planulation in *Pocillopora damicornis* occurs throughout the year in Hawai'i and the Marshall Islands (Richmond and Jokiel, 1984), but is seasonal in the Great Barrier Reef (Harriott, 1983) and Western Australia (Stoddart and Black, 1985). Further, the season in which this species spawns differs between these two areas. Tanner (1996) points out the seasonal nature of planulation in *Stylophora pistillata* and *Seriatopora hystrix* as well as *Pocillopora damicornis* in the southern Great Barrier Reef. *Stylophora pistillata* also planulates seasonally in the Red Sea (Rinkevich and Loya, 1979) but year round in Palau (Atoda, 1947). Whether these latitudinal and seasonal differences are related to a "simple" environmental factor such as temperature, or a complex set of environmental cues, understanding of such relationships would be a powerful tool in predicting responses of corals to environmental change.

We should not make generalized hind- or fore-casts of "coral" responses to environmental change until our understanding of coral reproductive biology is much deeper and broader than is currently the case. We must extend our knowledge of coral reproduction to encompass a larger fraction of the existing species, and deepen our understanding of the pathways that lead from spawning to settlement, before we can successfully predict how coral species will respond to environmental

change. These studies should focus on genera not yet studied. It may be hard to give up our favorite "white rats," but if coral diversity has any real importance, we should be prepared to learn from it. Additionally, we must view existing information from many perspectives. The multi disciplinary approach is an efficient way to achieve this goal and coral reef science is a particularly fertile ground for such efforts.

### Population biology

The term "population biology" as used here includes genetic, structural, and demographic aspects. This broad view recognizes one feature of this symposium--the idea that responses to environmental change will entail alterations in population structure (size, age, and genetics) (e.g., Lasker and Coffroth, 1999; Bak and Meesters, 1999), and spatial distribution (local, landscape and regional) (Lasker and Coffroth, 1999; Benzie, 1999; Karlson and Cornell, 1999), over a range of temporal scales (Done, 1999; Pandolfi, 1999). This definition allows discussion of some other, as yet poorly explored, potential avenues of adjustment in response to changing environments--hybridization, somatic mutation, and aspects of clonal population structure not discussed by Lasker and Coffroth (1999).

Veron (1995) pointed out that certain features of coral reproductive and population biology can produce complexity in population structure and evolution of corals. Veron's concept of reticulate evolution is primarily a biogeographically driven model (Pauley, 1996), but it was inspired partly by consideration of how broadcasting of gametes, particularly in mass spawning events, might promote hybridization among congeners or more disparate pairings. If hybridization is an important feature of coral reproduction, the population-level consequences could rapidly generate new genetic combinations with the potential for increasing the diversity of responses to environmental change. Additionally, our ideas about the integrity of coral species might be radically altered.

Experimental laboratory studies of corals have demonstrated that hybrids can be formed (Richmond, 1992; Willis et al., 1993, 1997). The speciose genus *Acropora* has provided data consistent with extensive hybridization (Kenyon, 1992; Wallace and Willis, 1994). Zoologists, unlike botanists, do not generally include hybridization in evaluating scenarios of

speciation, biogeography, and evolution, even though it is well known in animals (Bullini, 1994; Gill et al., 1995; Arnold, 1997). Certain characteristics of corals make them a likely place to look for a strong hybridization signal (Fautin, 1997).

Many corals are long-lived (e.g., Potts, 1984), but there is little direct investigation of this important topic from a biological perspective. Most age records for corals are from studies of skeletal structure and composition (Dunbar et al., 1994; Shen et al., 1996; Barnes and Lough, 1996; Fairbanks et al., 1997). These studies have documented colony ages of several decades to perhaps a few hundred years. However, to address the hybridization question, it is the age of the genetic line, not the colony, that is of concern (Potts, 1984; Gardner and Mangel, 1997). Clonal production of many colonies, even if each one is relatively short lived, may extend life of the genet, exposing it to a potentially wide range of temporal and spatial changes (Lasker and Coffroth, 1999).

The importance of genetic longevity to the question of hybridization lies in the extended period that hybrid genetic combinations may exist, even in the absence of sexual reproduction, thereby providing opportunities for chromosomal alterations that could restore fertility of hybrid genotypes (Kenyon, 1997). Recent modeling efforts suggest that under the appropriate set of population structural characteristics, senescence in genetic lines can be delayed for very long periods (Gardener and Mangel, 1997). Determination of how long such asexual lineages might persist is difficult, but terrestrial examples provide ages in excess of 10,000 years (Vasek, 1980; Lynch et al., 1999).

The second point relevant to the question of the importance of hybridization in corals is that in these animals there is no distinct separation of germ and somatic cell lines (Buss, 1987). Somatic cells with deleterious mutations will often undergo intra-colony selection (Michod, 1997) so that only stem cells with viable genomes transform into gametogenic lines. Because any stem cell has the potential to develop into a germ cell and to establish a new genetic line (Rinkevich, 1996), this within colony "pre-selection" could have crucial genetic and evolutionary consequences. Additionally a coral colony may have many reproductively active polyps at a time, increasing the number of sites for production and

incorporation of novel genotypes into gametes. The interplay between hybridization and somatic mutation was pointed out by Fautin (1997), who noted the great potential for somatic mutations to be incorporated into gametes in corals.

Besides the potential for promoting fertility in hybrids, somatic mutations may be part of the answer to another question in coral population biology—the conflicting results of grafting and genetic analyses within clones (Heyward and Stoddart, 1985, Resing and Ayre, 1985). Fautin (1997) noted that there is no empirical evidence that clonemates (i.e., asexually derived organisms which share a single common ancestor) will forever remain genetically identical. She also pointed out that not only could the non-congruence of the results from grafting and allozyme methods be explained, but the very differences between patterns observed in using the two techniques together might provide important insights into the structure of coral populations.

Yet another mode of genetic innovation is the formation of chimeras, organisms containing distinct genotypes from two or more sources, usually of the same species (Harvell, 1990). This phenomenon has recently been studied in red algae, where it appears to be relatively common (Munoz and Santelices, 1994; Santelices et al., 1996). Coalescence of propagules and the subsequent formation of chimeras also occurs in scleractinians, where the resulting organism exhibits faster growth rates and achieves a larger size than unitary colonies (R. Richmond, personal communication, cf. *Science*, 1998, 279:808). These scenarios may still appear exotic to zoologists, but they are the stuff of plant evolutionary biology and deserve to receive serious attention by coral biologists.

The potential for hybrid origin of species has attracted much attention among coral biologists as an explanation for high levels of species diversity, but it is also important to remember that only three or four scleractinian genera are likely candidates for hybridization as a major mode of speciation. Most coral genera contain only a handful of species (Veron, 1995). It is also important to realize that while hybridization has the potential to increase diversity by promoting speciation thereby sharpening biogeographical provinciality, it can also keep diversity low

by enhancing gene flow among populations, blurring species boundaries, and producing geographically widespread "species complexes." Whichever way hybridization takes any group, the resulting entities might respond to environmental change in ways not easily predicted, given our current level of understanding coral taxonomy and biogeography.

We must broaden our understanding of the genetic nature of coral populations if we are to have a basis for predicting what potential exists for response to environmental change on all scales. This understanding of the genetic structure of coral populations must deal with the question of currently accepted widespread "species" at local, landscape, and regional scales. The relative importance of hybridization and intra-clonal genetic variation in corals should be quantitatively assessed over appropriate temporal and spatial scales.

### Coral symbioses

The most studied reef symbiosis is that between the dinoflagellates termed zooxanthellae and their invertebrate hosts (Trench, 1992, 1993). The physiology of the relationship in terms of photobiology and material exchanges between the partners has been studied since the 1950s and is covered in numerous reviews (Muscatine, 1974, 1980, 1990). The reproductive biology of these dinoflagellates is a striking counterpoint to the "anything goes" picture for many of the host animals. Reproduction of zooxanthellae is currently thought to be exclusively by simple mitotic cell division; there is no evidence of sexual recombination (Trench, 1993). While future work may alter our view of this aspect of zooxanthella biology, it currently appears that the array of potential algal symbionts consists of a number of clonal lines. Determination of the number, identity, and relationship among these symbiotic algal lines and their free living stages, is still in its infancy, but this knowledge will be vital to understanding coral evolution, ecology, biogeography, and outlooks for the future.

Two approaches to the question of zooxanthella diversity are currently used (Trench, 1997). The first represents a classical taxonomic approach based on morphological, biochemical, and, to some extent, behavioral characters to identify and name taxonomic entities (Schoenberg and

Trench, 1980; Trench and Blank, 1987; Banaszak et al., 1993). This approach has identified 23 "zooxanthella" taxa, only 2 of which are known to occur in scleractinians (Trench, 1993). While this approach has given insights to the place(s) where "zooxanthellae" fit in the overall systematic picture of dinoflagellates, we are not yet at the stage where this information can be used in ecological or evolutionary study of corals. Because this approach implicitly assumes that a zooxanthella taxon is restricted to a single host species, its relevance to current models of coral symbiosis is not clear.

The second approach uses molecular characters to define units, with no attempt to provide nomenclatural precision (Rowan and Powers, 1991, 1992; McNally et al., 1994). This broad-brush approach has changed our understanding of how symbioses involving zooxanthellae might function (Rowan and Knowlton, 1995). The possibility of an ecological rather than a taxonomic basis of the zooxanthella-host pairing was suggested long ago (Kinzie and Chee, 1979), but the evidence at that time was weak. Recent work opens this possibility up to entirely new levels of study. Regardless of approach, it is now clear that there are multiple potential symbionts in nature, and that the symbiosis is more complex than previously supposed.

The dynamic nature of the relationship can be seen from different perspectives and on several spatial and temporal scales. Corals release about one percent of their algal complement each day (Hoegh-Guldberg et al., 1987; Stimson and Kinzie, 1991). This turnover suggests that the algal population in a host should be viewed as a dynamic, and perhaps non-equilibrium, system. It has been suggested that the phenomenon of coral "bleaching" might not be simply a breakdown of a stable relationship that serves as a symptom of degenerating environmental conditions. The loss of algal symbionts may be part of a mutualistic relationship on a larger temporal scale, wherein the identity of algal symbionts changes in response to a changing environment (Buddemeier and Fautin, 1993; Buddemeier et al., 1997). The recent report of a dynamic interaction between multiple algal populations within a single host colony suggests complexity and dynamism in the algal-host relationship at the scale of the colony (Buddemeier, 1997; Rowan et al., 1997), while Baker and Rowan (1997) suggest there is also an important regional component to the

structure of the symbiotic system.

Two things can be learned from these new perspectives. First is the potential for a mode of adjustment to environmental change that is both rapid and flexible. To discover how much of this potential is actually achieved in nature, we will need to learn about: 1) the population dynamics of the various algal strains themselves, 2) the physiological capabilities of different potential algal symbionts, and 3) the capabilities of the different host-algal combinations. Gates and Edmunds (1999) explore these possibilities from the perspective of acclimation at the scale of the host organism.

Secondly, we must begin treating the algal-host system not just on the scale of the colony, as a simple physiological joint effort, but also at the community scale. At this larger scale, complex interactions exist among multiple populations of algae that are spatially structured into free living and within-host compartments, as well as the relationship between a host and algae it harbors at a point in time. The potential of this complex and dynamic mutualistic association to adjust to environmental change cannot be assessed until we have come to grips with the full extent of the symbiosis.

Future effort should be directed at bringing together algal geneticists, systematists and physiologists to map out the menu of potential algal symbionts available to invertebrate hosts, and the ecological abilities of the resulting symbiotic entities. We must determine the basic natural history and population biology of zooxanthellae, both in their hosts and free-living on reefs. Zooxanthellae must be viewed as part of the reef community as well as partners in specific symbioses. Development of rapid techniques to allow identification and quantification of algal types within hosts and in the field would do much to advance our understanding of this system.

### Coral community ecology

The study of how communities in the past responded to environmental changes holds important lessons for predicting the future of coral reefs. We learn from paleontology that when global change alters conditions for organisms (on a regional if not local scale), the species appear to respond

individually (Jablonski and Sepkowski, 1996; Pitelka et al., 1997). That is, communities do not migrate over the globe--species do. If this individualistic response proves to be the case for modern coral reefs, we can predict that reef communities in the future will consist of species occurring together in assemblages that may be quite unlike what we see today. One potential way to learn more about what the reefs of the future might look like is by study of reef systems at the margins rather than at the center of modern reef distribution. In these locations we often find functionally intact assemblages, including corals, that are very unlike what we think of as "normal, healthy" reefs (Smith, 1981; Coles, 1988; Tribble and Randall, 1986). Additionally, there is some indication from modern reefs that when environmental conditions change, disruption of certain interspecific linkages occur before any noticeable changes in abundance of dominant species (Reese, 1993). This is particularly true on reefs because of the very long lives of many important reef-building corals (Potts, 1984; Bak and Meesters, 1999), since individuals may persist long after the species fails to recruit. Alterations in community function could occur well before changes in abundance of dominant species are noticed. Such threshold effects can have important implications in ecological systems (Allen and Hoekstra, 1992).

Ecological processes can be evaluated at several levels. Recent thinking in ecology has tended to break down traditional viewpoints that have isolated autecology, population biology, community and ecosystem viewpoints (Allen and Hoekstra, 1992; Jones and Lawton, 1995). One result of this approach is that ecological functions are now being studied simultaneously at levels ranging from the individual or species, to the ecosystem or landscape scale, providing a more holistic (and perhaps realistic) view of natural processes (Hatcher, 1990). The unanswered question for coral reef managers and ecologists is what is essential coral reef function? Is it deposition of wave-resistant carbonate structures? accumulation of organic carbon or biomass? maintenance of high species diversity? production of propagules in a metapopulation context? Until we determine which of these, or other functions are essential for "reefness," the question "is this reef healthy?" will remain unanswerable.

High species diversity, a hallmark of coral reef systems, is a mixed blessing for students of reefs. The sheer number of species means that

most studies deal with only a few of the most common, attractive, apparent, or easy to study representatives. The possibility that reef communities of the future may present novel species combinations means that our ability to predict functional aspects of these new communities will be only as good as our understanding of the ways existing communities function in a general sense rather than knowledge of how a specific aggregation of species functions today. A question of interest to community ecologists is whether all, most, or only a few of the species present in a community are essential for community function (Tilman, 1997; Tilman et al., 1997; Hooper and Vitousek, 1997).

Bak and Meesters (1997) have asked whether all the species that occur on a reef are necessary for the reef to exist or function. A similar question has been asked of algal communities--"are algal species really just 'noise' in the ecology of communities?" (Hay, 1994). Experimental work in terrestrial systems has provided evidence that simple measures of species diversity--the sort commonly used by reef scientists--may be a poorer predictor of community function than the diversity of functional groups or the presence or absence of specific functional groups. Is the concept of functional groups applicable to reefs (Steneck, 1988; Done, 1999), or are reef species either so functionally similar that redundancy is the overriding characteristic, or else so diverse that they cannot be agglomerated into more tractable units? Certainly we know that high diversity in and of itself is neither necessary nor sufficient to produce a reef structure and the associated functioning community. Species-poor reefs near the margins of scleractinian distribution (e.g., Hawai'i, Bermuda, the Arabian Gulf, Clipperton Island, S. E. and S. W. Australia) can be--as far as we can tell at our present state of knowledge--as "reefal" as systems with many more species. On the other hand, there are suggestions that some reefs with low redundancy may be less able to withstand perturbations (i.e., they are less resistant) or to recover from impacts (i.e., they are less resilient). In the Caribbean, the major framework builders are broadcasting species in the genera *Acropora* and *Montastrea* (Szmant, 1986; Bak and Meesters, 1997) with two and four important reef-building species respectively. Impacts from a range of sources (competition with algae, "diseases," etc.) have affected these species to the apparent detriment of total reef community structure in some regions of the Caribbean (Porter and Meier, 1992; Hughes, 1994;

Santavy and Peters, 1997). It is possible that in times before major human impacts (Jackson, 1997), these large, long-lived broadcasting species could maintain their importance in the community by recruitment events that occurred at long but dependable intervals. Today, these major Caribbean framework builders recruit rarely, if at all (Smith, 1992; Bak and Meesters, 1997, 1999; Kuta and Richardson, 1997), with the result of either a shift in community dominance (Hughes, 1994; Aronson and Precht, 1997) or a general decline in reef community integrity. The low recruitment levels of important reef-builders that are broadcasters seems, at least today, to be generally true in all but the richest reef areas (i.e., the GBR) (Birkeland et al., 1981; Rogers et al., 1984; Sammarco and Andrews, 1988; Fisk and Harriott, 1990; Bak and Meesters, 1997). Is this a recent phenomenon, reflecting some--as yet--unidentified global scale change in reef ecology, or is it due to fact that the average temporal span of a human study is simply not long enough to capture the sporadic, but essential, events of successful recruitment of major framework builders? This question is of utmost importance in predicting future scenarios for today's reefs. The fate of reefs that had been dominated by these long-lived but infrequently recruiting species in a future world where the frequency of disturbances greatly exceeds the "generation time" is uncertain at best (Potts, 1984).

We tend to impose human time frames on systems where this is inappropriate (Hoekstra et al., 1991). We are only now beginning to discover what time frames are appropriate for the study of coral reefs on long (Potts, 1984), intermediate (Pandolfi, 1999) and short (Bak and Meesters, 1999; Done, 1999) temporal scales. It is clear that the definition of a healthy reef as "what it looked like when I started diving" is fraught not only with hubris but strong temporal bias. Here is a fruitful place for collaborative thinking between paleontologists and neontologists.

Evaluating species assemblages in terms of a product is a way of quantifying system function, and so, by extension, community integrity and ecosystem processes (Allen and Hoekstra, 1992). Outputs can be measured as biomass (Tilman, 1997), calcium carbonate deposition (Smith, 1983), or energy (Hatcher, 1990). Several experimental studies of community function have used output as a measure of stability (Sternler, 1995; Johnson et al., 1996; Tilman et al., 1997). Some beginnings have

been made in modeling energy flow in specific reefs (Grigg et al., 1984), but use of these models has not generally been exported for use in other reef systems, despite the striking uniformity of coral reef performance noted by Kinsey (1983). A characteristic of reefs is that the production of biological components is tightly linked, both biologically and stoichiometrically, with the production of the inorganic carbonate structure (Hatcher, 1988, 1990; Kinsey, 1983). However, using system output to evaluate the status of reefs requires serious thought be given to how the output variable that is chosen agrees with what we really want to know about the system. Using diversity as a catch-all measure, as is frequently the case, is not likely to tell much about how a reef might provide food to local residents or physical protection to coastal habitations, although it might be useful to evaluate sites for tourism. With proper consideration it may be possible to devise a metric based on system processes or products that would provide a suitable gauge for evaluating system responses to environmental change.

The first step toward eliminating the red herring of "reef health" is determining the structural and functional aspects of reefs that we value. For each of the processes deemed to be important for reef function, we must define the relevant temporal and spatial scales. Study of reefs and reef-like assemblages in marginal regions may point out which, if any, functional groups are missing and whether their absence impacts community or ecosystem function.

## SUMMARY

We are probably not ready to hindcast, let alone forecast, the relative success of different reproductive modes because our current understanding of coral reproductive biology is so incomplete. However, existing observations do suggest that broadcasting corals, particularly many that are major contributors to reef structure, may not be replacing themselves in certain areas. Hybridization in corals may have important consequences both for evolution and biogeography and needs more study, as does the potential for somatic mutation in long-lived genetic lines of corals.

We currently have neither the depth nor the breadth of basic knowledge to

evaluate the most basic features regarding the ecological, biogeographical, or phylogenetic effects on the specificity (or lack of it) of the zooxanthella-host relationship. While there is a tradition of studying the trophic relationship between zooxanthellae and their hosts, our current knowledge may be rendered useless if it is discovered that a multiplicity of potential algal symbionts exists and that there are differences among them in their ability to use light, take up nutrients, and pass fixed carbon to their hosts.

We have barely started teasing apart the community linkages responsible for reefs as we see them today, let alone how coral reef communities might respond to large- and small-scale environmental changes. Experimental work to identify the strong inter-actors and the critical linkages among reef species is a necessary first step. Here it is of paramount importance that boundaries between coral biologists, phycologists, ichthyologists, microbiologists, etc. be broken down. Until this happens coral science will not achieve its potential as an interdisciplinary science, nor will it provide the information necessary to devise workable and effective management measures.

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