Kansas Geological Survey

REEF SCIENCE: ASKING ALL THE WRONG QUESTIONS IN ALL THE WRONG PLACES?

Robert W. Buddemeier[1] and Robert A. Kinzie III[2]

[1]Kansas Geological Survey, University of Kansas, Lawrence, KS 66047
[2]Zoology Department, University of Hawaii, Honolulu, HI 96822

[This is the text of a paper presented at the 8th International Corel Reef Symposium, Panama City, Panama, June 24-29, 1996]

KANSAS GEOLOGICAL SURVEY
OPEN-FILE REPORT 97-13

FEBRUARY 1997

GEOHYDROLOGY

The University of Kansas, Lawrence, KS 66047 Tel. (913) 864-3965

REEF SCIENCE: ASKING ALL THE WRONG QUESTIONS IN ALL THE WRONG PLACES?

Robert W. Buddemeier[1] and Robert A. Kinzie III[2]

[1]Kansas Geological Survey, University of Kansas, Lawrence, KS 66047
[2]Zoology Department, University of Hawaii, Honolulu, HI 96822

ABSTRACT

Both rediscovered wisdom and recent findings challenge long-standing assumptions about corals, reefs, and research strategies. Critical issues include: (1) The "healthy" coral reef community -- our present concept may be an anomalous and unimportant environment on evolutionary time scales; (2) The life history and evolutionary implications of clonality, sexual vs. asexual reproduction, and hybridization, particularly in relation to adaptation and acclimation; (3) The potentially wide variety and lability of coral-algal symbioses, and the genetic diversity of both partners; (4) Carbonate chemistry and the benthos — CO_2 control of photosynthesis, $CO_3^=$ control of calcification; and (5) The equivocal role of nutrients in reef development and decline. Items 2 and 3 suggest that reef communities may be far more plastic than previously thought; items 4 and 5 require rethinking reef biogeochemistry, and new levels of experimental sophistication. The resulting picture of corals and reefs is substantially different from the traditional view, with major implications for conservation and management as well as research.

INTRODUCTION

As the present and probable future extent of human impacts on the natural environment of the planet become ever clearer and ever more frightening, issues, organisms, and ecosystems queue up for their turn in the conservation spotlight. Corals have become the "doe-eyed invertebrates" (C. M. Eakin, pers. comm.), and coral reefs are widely touted as "rainforests of the sea," in emulation of the terrestrial ecosystem best equipped with fan clubs, lobbyists, and websites.

Attention to environmental threats and to the imperatives for improved understanding, conservation, and resource management are unquestionably good. However, with this attention come demands for popular explanations and for management strategies and tactics that outstrip our understanding of the system we would save. Gaps in scientific understanding combine with ingenuous anthropocentrism few mm. In fact, sea level rise or fall of a cm/yr or more is in fact a much more "normal" environment (Fig. 1 in Quinn (1991))-- and with this change comes order-of-magnitude variations in the shallow benthic area in which reefs can develop. It has been suggested that up to 40% of present reef area may be degraded beyond recovery within 20 years (Wilkinson 1993). If we assume that reef area is proportional to benthic surface area within the latitude and depth ranges of coral reefs, then Figure 1 suggests that reef area will be ≥40% less than at present at any sea level more than about 20 m below present -- conditions representative of >80% of the last 120,000 years!

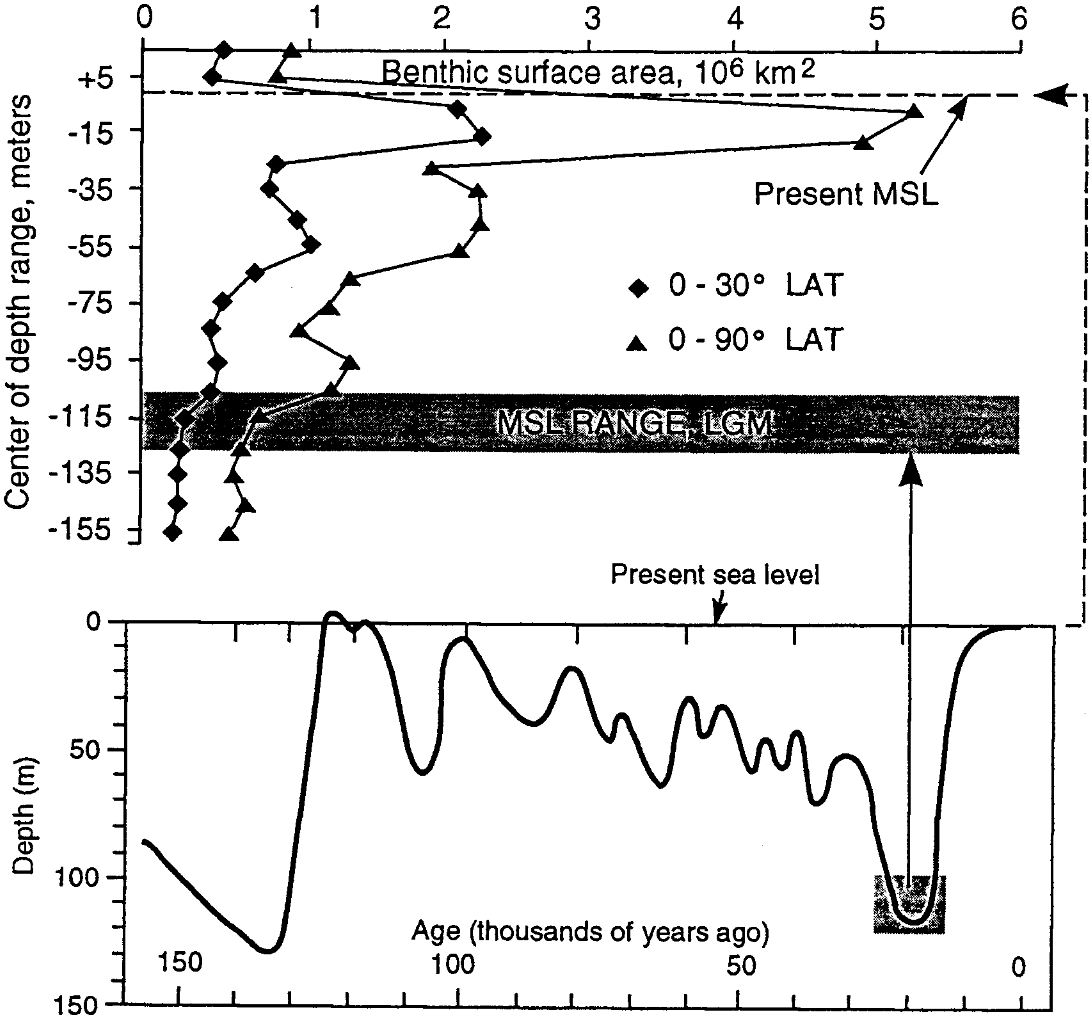

Figure 1: Sea level fluctuations during the late Quaternary (lower graph) are typical of the last several million years. The benthic area available for reef development (0 to -20 m depth range in the 0-30° plot, upper graph) is no more than 50% of the present value at "average" sea level, and may be as little as 10% at extreme lowstands.

We may be fixated on reef communities as big carbonate accumulations because: 1.) that is what we see now, although these accumulations result from recent anomalous sea-level history; and, 2.) that is what is best-preserved (rather than most representative) in the geologic record. We suggest that these may be extraneous and even quasi-pathological features in terms of the biological propagation of species and communities over geologic and evolutionary time. Like obesity; a massive reef accumulation may be the result of remaining stationary for too long under good conditions. The focus on oceanic reefs in oligotrophic waters has led to the perception that reefs closely associated with continental margins are somehow second rate -- in spite of the fact that it has been postulated that much of the species diversity of corals is a consequence of shelf dynamics (Potts 1985). The "right places" to study the survival and dynamics of reef ecosystems are more likely to be the not-quite-reefs, the sort-of-reefs, and the used-to-be-reefs.

Wrong Questions

Wrong questions flow naturally from irrelevant contexts (= wrong places). The erroneous assumption that a specific reef type represents "health" leads to research questions aimed at elucidating the environmental conditions that have led to this "optimal" reef development, but even more dangerous (because less testable) is the implicit biological assumption built into: "How are the species that make up this community co-adapted to enhance or stabilize this optimal assemblage?" We suggest that the old argument about whether the "tropics are stable because they are complex" or "tropics can afford to be complex because they are stable" is wrong on both sides -- reef environments are not stable, and the important question is: "What are all these supposedly co-adapted organisms doing when the 'optimal assemblage' isn't around?" (Grigg and Maragos 1974).

NUTRIENTS -- GOOD, BAD OR UGLY

The emphasis on "pristine" oligotrophic conditions as the *sine qua non* of "healthy" reef development has led to the generalization that higher nutrient levels are intrinsically damaging to coral function. This assertion is made (Muscatine and Porter 1977) in spite of evidence that not only can corals grow well at high nutrient levels, but also that scleractinian corals can persist in close juxtaposition to macroalgae that are commonly regarded as superior competitors in high nutrient situations (e.g. the Houtman Abrolhos Islands (Smith 1981)).

We know that high-nutrient environments can enhance bioerosion, and in the past seem to have resulted in the inhibition or destruction of reef and carbonate platform formations (Hallock 1988; Hallock and Schlager 1986) -- but this observation relates primarily to the fate of the reef community products (carbonate accumulation), not necessarily of the organisms -- if carbonate is a waste product, the organisms may not care much what happens to it. We know that elevated nutrients may enhance the competitive ability of non-calcifying benthos, resulting in overgrowth or replacement of coral reef communities (Grigg and Dollar 1990; Smith et al. 1981) - but we also know that this is not inevitable (Kinsey 1991)). Nutrient levels affect the populations and physiology of the symbiotic algae (Dubinsky et al 1990), but these studies have generally not addressed the potential time scales and mechanisms (e.g., algal exchange) involved in acclimation. We even have available to us an ocean-scale comparison experiment in the form different levels of nutrient adaptation in the Caribbean and the Indo-Pacific (Birkeland 1987; Wilkinson 1987).

The results of our nutrient preoccupationís have been a succession of disagreements supported on all sides by the results of experiments that are neither equivalent to each other nor representative of the actual time scales and organism or community characteristics involved in real nutrient responses.

Wrong places
Short term laboratory or field experiments directly extrapolated to ecosystem scales of space, time, and complexity (reductionist approaches require a valid model for re-integration of results).

Wrong question(s)
"What is the effect of (ambient water) nutrient concentration rates on......." (without regard to loading, inventory, delivery rates, uptake rates, community structure/function, specification of time scales, etc. etc.).

LIFE HISTORY, CLONALITY, AND REPRODUCTION

Much biological thinking relative to coral reef animals comes from a thoroughly zoological background with emphasis on physiological, morphological and behavioral responses of individuals, and on the genetics of sexually reproducing individuals. This ignores the life history and evolutionary implications of clonality, sexual vs. asexual reproduction (Fautin 1996), hybridization (Veron 1995), and somatic mutation, particularly in relation to adaptation and acclimation (Buddemeier et al. 1995).

Wrong (conceptual) places
(1) Intra-specific sexual reproduction; and
(2) Phylogenetic analysis limited to morphospecies.

It has long been recognized that corals and other reef organisms are colonial, and recent work has established that many important reef animals are extensively clonal. These observations clearly point to the importance of asexual or vegetative reproduction -- typically regarded by anthropoid researchers as what animals resort to when they can't have sex. In fact, these modes of reproduction and their combination with sexual reproduction are probably central determinants of the character of reefs and reef organisms. The potential for rapid build-up and transmission of somatic mutations by asexual reproduction provides a mechanism by which selection can operate within the lifetime of the organism (Fautin 1996) or clone (Buddemeier et al. 1995), as is the case with many terrestrial plants (Gill et al. 1995).

The process of sexual reproduction has also been found to be much more flexible than would be expected on the basis of terrestrial zoologists' concepts of a species as a reproductively isolated population. Mass spawning events clearly offer opportunities for hybridization, and a growing body of experimental evidence confirms the possibility of hybridization (reviewed by (Veron 1995), pp 83-84).

The existence of well-established mechanisms, both sexual and asexual, for introduction of and selection on genetic diversity in corals seems at odds with the apparent evolutionary stability of scleractinian "species" based on the fossil record (Veron 1995). This apparent conflict is the result of neglecting the reticulate nature of coral evolution; if introgression is a common phenomenon, then a species-specific focus will provide misleading results. This is exemplified by the growing realization that what was once regarded as single species may represent suites of "sibling species" (Knowlton 1993) -- these closely related populations may represent "evolutionary experiments" in progress, with outcomes (recombination, extinction, or further divergence) -- and hence their ultimate phylogenetic significance -- still uncertain (O'Hara 1993).

Why is this important? In terrestrial and temperate aquatic communities, as environmental conditions rapidly change we see major shifts in species composition that are interpreted as shifts in community structure and function, and evidence of responsiveness of the system (Pimm 1991). On reefs we see what appear to be the same species, or complexes of species, or even assemblages of species persisting through repeated major changes (Jackson et al. 1993; Pandolfi 1996), which is interpreted as either extreme stability or inability to respond.

In coral reef ecosystems the tracking of environmental changes may be by survival of some clones (or hybrids) over others. The end result might be a very different genetic landscape with little or no change in apparent species composition or relative abundance - metrics we often use to gauge reef health.. As long as environmental variation stays within the tolerance range of the "extended species," the community will appear stable to the observer of morphospecies. However, the system may be ramping up to a threshold (which may not be noted because the shifts are occurring among clones within species or among cryptic species) at which the last available clone type can't track changes any more, and a major restructuring event takes place apparently triggered by a small environmental perturbation. This provides a genetically-based mechanism for catastrophic transitions (Buddemeier and Hopley 1988) in reef communities. It also raises serious questions about the ability of simple descriptive community monitoring to detect trends in ecosystem health.

The questions we raise cannot be adequately addressed solely by reductionist, laboratory-based studies of conventionally defined morphospecies. We therefore nominate as generic "**Wrong Questions**" anything that results in an answer in any of the following (implicit or explicit) formats:

(1) By intensive study of specimens collected from a well-defined spatial and temporal regime, we have determined the characteristics of the species to be..."

(2) "Based on the responses and characteristics of (specimens of) this species, we conclude that scleractinian corals..."

(3) "Through intensive study of a particular process under carefully controlled experimental conditions we can say that corals will...."

CORAL-ALGAL SYMBIOSES AND GENETIC DIVERSITY

Related to the problems associated with the extensively clonal nature of many reef organisms is how these different clades interact with each other. Recent work indicates that there is a complex skein of associations between several lines of zooxanthellae and two cryptic coral species (Rowan and Knowlton 1995). If this sort of flexibility in coral-algal associations is general, experiments on particular sets of coral+alga (termed "ecospecies" by Buddemeier and Fautin (1993)) will not give results representative of the larger suite of symbiotic associations, or of what might be occurring on reefs where the lability and plasticity of the symbiosis could be more generally expressed (Ware et al. 1996).

Much effort has been put into determining, often in a very reductionist way, "the" relationship between algal symbionts and their hosts. The effort put into such studies would be warranted if we were certain that the entities participating in the symbiotic relationship being studied were stable and representative of what occurs on reefs. However, in light of the flexibility in the system, the results of these studies, elegant as they might be, must now be viewed with caution verging on skepticism. A reductionist, laboratory-based approach to the study of symbiosis is the antithesis of what is needed to understand the ecological and evolutionary implications of the complex and shifting confederations that may exist between algal symbionts and invertebrate hosts.

Wrong place

For studies of characteristics related to the algal symbiosis, any host-symbiont pair that is not fully characterized with respect to present partners, with at least some consideration of the potential for alternative partners.

Wrong questions

Same as for the preceding section (Life History, etc.), but with emphasis on failure to consider the genetic, taxonomic, and functional variability in the algal partner and in host-alga interactions --- both at one time and through time.

CARBONATE CHEMISTRY AND THE BENTHOS

It has long been known that light- (or symbiotically-) enhanced calcification is a reality in terms of the geology and biogeography of reef-forming organisms. It has also long been recognized that calcification consumes carbonate ions and is therefore (in the bicarbonate-dominated marine environment) a source of carbon dioxide (Morse and Mackenzie 1990). It has been suspected (Smith and Buddemeier 1992; Smith and Pesret 1974) that carbonate saturation state is a control on both organism and community calcification; experimental evidence confirming that is now accumulating (Agegian 1985; Marubini and Atkinson, in prep.; Bourge et al. 1996). In spite of abundant quantitative evidence based on past and present chemical budgets and experiments, contemporary reef researchers find it convenient to ignore the critical role played by calcification and the inorganic chemistry of carbon.

Although we may have uncertain definitions of reef health, we are reasonably confident that the transition from a calcification-dominated system to a system primarily describable in terms of organic carbon budgets represents a major deterioration -- and probably collapse -- of a coral reef ecosystem (e.g., Hughes (1994)). Efforts to portray reefs as carbon dioxide sinks (Kayanne et al. 1995) have the potential to define as normal or desirable some of the most critical symptoms of reef decline (Buddemeier 1996).

Similarly, revisionism focused on the role of calcification (Marshall 1996) in the coral-algal symbiosis and community structure and function has the potential to distract attention from a critical and poorly understood environmental control on reef function (saturation state) that almost certainly undergoes significant variation on a variety of time scales as a result of both natural (Mackenzie and Agegian 1989; Sanyal et al. 1995) and anthropogenic (Smith and Buddemeier 1992) climate change.

Wrong place(s)
Studies of symbiotic organisms that do not calcify, or that do calcify but in which no attention is paid to the rates, mechanisms, or patterns of calcification; short-term community level studies that do not define the system under study or scale up to community-relevant scales of space and time.

Wrong question(s)
Any questions that address (skeletal) growth or calcification rate without quantitative consideration of the carbonate-system chemistry of the water. Any questions that ignore the effects of either carbonate or carbon dioxide uptake on the other component of the coral-algal carbon cycle. Those that address a question (e.g., climatic or geologic source-sink relationships) at an inappropriate scale (e.g., short-term fluxes or metabolism).

SUMMARY

Phylogenetic trees have been likened to cartographic maps (O'Hara 1993) in that no single scale, projection, or selection of attributes is uniquely true or -- more importantly -- useful for all applications. We suggest that use of coral alpha taxonomy based on host morphology for addressing the larger issues of evolution, symbiotic interactions, and biogeography is like using a collection of city street maps to navigate across a largely non-urban continent. The detail is so disconnected and irrelevant that we end up proceeding by dead reckoning -- but we continue to cite the street maps because they are our only published authorities!

The evidence suggests that both organisms and reef communities may be far more plastic than previously thought. We suggest that the answers to how reefs and corals survive and develop is better found by studying the range of intermediate states rather than end-members in a continuum, and that it is important to recognize that the environmental conditions we consider "normal" are in fact end-members in the geological, climatological, and evolutionary scheme of things.

It is time to rethink reef biogeochemistry, and to integrate our fragmented view of N, P, and especially C metabolism over time and space scales relevant to real reef communities and to organisms not isolated in laboratory containers. New levels of experimental sophistication are required, but this needs to be integrative and large-scale sophistication to qualify, explain, and apply the findings of reductionist science that are conventionally assumed to represent "sophistication."

There already exists a broad-brush, "top-down" picture of corals and reefs that is substantially different from the view based on "bottom-up" assembly of the bits and pieces of individual research. We consider it an urgent challenge to develop the broader view into an effective tool for both conceptualization and quantitative hypothesis development, as it has major implications for conservation and management as well as research.

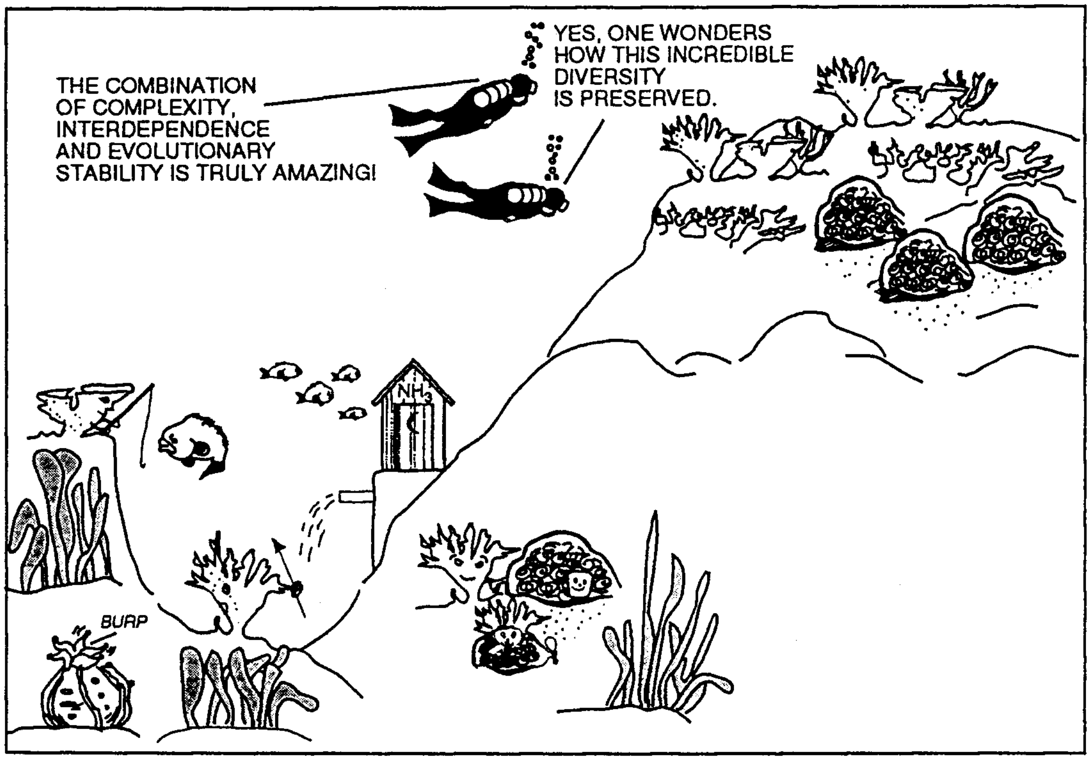

Figure 2: Gullible human scientists are easily fooled by the distraction displays of cunning invertebrates.

ACKNOWLEDGMENTS

D. Archer supplied the benthic surface area data, D. Fautin provided review and advice, M. Schoneweis, M. Miller and A. Ow assisted with manuscript preparation.

REFERENCES

Agegian CR (1985) The Biogeochemical Ecology of_*Porolithon gardineri* (Foslie) [Doctoral dissertation]. University of Hawaii, Honolulu

Birkeland C (1987) Nutrient availability as a major determinant of differences among coastal hard-substratum communities in different regions of the tropics. In: Birkeland, C (ed) Comparisons between Atlantic and Pacific Tropical Marine Coastal Ecosystems: Community Structure, Ecological Processes, and Productivity. UNESCO, Paris, pp 45-97

Bourge I, Gattuso J-P, Frankignoulle M (1996) Effect of aragonite saturation on calcification of zooxanthellate scleractinian corals. Proc 8th Int Coral Reef Sym, in press

Buddemeier, RW (1996) Coral reefs and carbon dioxide. Science 271:1298-1299

Buddemeier RW, Fautin DG (1993) Coral Bleaching as an Adaptive Mechanism: A Testable Hypothesis. BioScience 43:320-326

Buddemeier RW, Fautin DG, Ware JR (1996) Acclimation, adaptation, and algal symbiosis in reef-building corals. In: den Hartog, K (ed) Proc 6th Int Conf on Coelenterate Biology, Noordwijkerhout, The Netherlands, in press

Buddemeier RW, Hopley D (1988) Turn-ons and turn-offs: causes and mechanisms of the initiation and termination of coral reef growth. Proc 6th Int Coral Reef Symp 1:253-261

Dubinsky Z, Stambler N, Ben-Zion M, McCloskey L, Falkowski PG, Muscatine L (1990) The effects of external nutrient resources on the optical propoerties and photosynthetic efficiency of *Stylophora pistillata*. Proceedings of the Royal Society of London B239:231-246

Fautin DG (1996) Cnidarian reproduction: assumptions and their implications. In: den Hartog, K (ed) Proc 6th Int Conf on Coelenterate Biology, Noordwijkerhout, The Netherlands, in press

Gill DE, Chao L, Perkins SL, Wolf JB (1995) Genetic mosaicism in plants and clonal animals. Annual Reviews of Ecology and Systematics 26:423-444

Grigg RW, Dollar SJ (1990) Natural and anthropogenic disturbance on coral reefs. In: Dubinsky, Z, (ed) Coral Reefs. Elsevier, Amsterdam pp 439-452.

Grigg RW, Maragos JE (1974) Recolonization of hermatypic corals on submerged lava flows in Hawaii. Ecology 55:387-395

Hallock P (1988) The role of nutrient availabity in bioerosion: Consequences to carbonate buildups. Palaeogeography, Palaeoclimatology, Palaeoecology 63:275-291

Hallock P, Schlager W (1986) Nutrient excess and the demise of coral reefs and carbonate platforms. Palaios 1:389-398

Hughes TP (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. Science 265:1547-1551

Jackson JBC, Jung P, Coates AG, Collins LS (1993) Diversity and extinction of tropical American mollusks and emergence of the isthmus of Panama. Science 260:1624-1626

Kayanne H, Suzuki A, Saito H (1995) Diurnal changes in the partial pressure of carbon dioxide in coral reef water. Science 269:214-216

Kinsey DW (1991) The coral reef: an owner-built, high-density, fully serviced, self-sufficient housing estate in the desert -- or is it? Symbiosis 10:1-22

Kinzie RA (in press) Caribbean contributions to coral reef science. In: Benson K, (ed) Proc 5th Int Congr History of Oceanography, San Diego, CA, 1994

Knowlton N. 1993. Sibling species in the sea. Annual Reviews of Ecology and Systematics 24:189-216.

Mackenzie FT, Agegian CR (1989) Biomineralization and tentative links to plate tectonics. In: Crick RE (ed) Origin, Evolution, and Modern Aspects of Biomineralization in Plants and Animals. New York: Plenum Press. p 11-27.

Marshall AT (1996) Calcification in hermatypic and ahermatypic corals. Science 271:637-639

Marubini F, Atkinson MA (in prep) Effects of nitrate and pH on coral calcification.

Morse JW, Mackenzie FT (1990) Geochemistry of Sedimentary Carbonates. Elsevier, New York

Muscatine L, Porter J (1977) Reef corals: mutualistic symbioses adapted to nutrient-poor environments. Bioscience 27:454-459

O'Hara RJ (1993) Systematic generalization, historical fate, and the species problem. Systematic Biology 42(3):231-246

Pandolfi JM (1996) Limited membership in Pleistocene reef coral assemblages from the Huon Peninsula, Papua New Guinea: constancy during global change. Paleobiology:in press.

Pimm SL (1991) The Balance of Nature? University of Chicago Press, Chicago

Potts DC (1985) Sea-level fluctuations and speciation in Scleractinia. Proc 5th Int Coral Reef Congr

4:127-132

Quinn TM (1991) The history of post-Miocene sea level change: Inferences from stratigraphic modeling of Enewetak Atoll. Journal of Geophysical Research 90(B4):6713-6725

Rowan R, Knowlton N (1995) Intraspecific diversity and ecological zonation in coral-algal symbiosis. Proc Natl Acad Sci USA 92:2850-2853

Sanyal A, Hemming NG, Hanson GN, Broecker WS (1995) Evidence for a higher pH in the glacial ocean from boron isotopes in foraminifera. Nature 373:234-236

Smith SV (1981) The Houtman Abrolhos Islands: carbon metabolism of coral reefs at high latitude. Limnology and Oceanography 26:612-621

Smith SV, Buddemeier RW (1992) Global change and coral reef ecosystems. Annual Reviews of Ecology and Systematics 23:89-118

Smith SV, Kimmerer WJ, Laws EA, Brock RE, Walsh TW (1981) Kaneohe Bay sewage diversion experiment: Perspectives on ecosystem responses to nutritional perturbation. Pacific Science 35:279-402

Smith SV, Pesret F (1974) Processes of carbon dioxide flux in the Fanning Island lagoon. Pacific Science 28:225-245

Veron JEN. 1995. Corals in Space and Time. Sydney: UNSW Press, Sydney

Ware JR, Fautin DG, Buddemeier RW (1996) Patterns of coral bleaching: modeling the adaptive bleaching hypothesis. Ecological Modeling 84:199-214.

Wilkinson CR (1987) Interocean differences in size and nutrition of coral reef sponge populations. Science 236:1654-1657

Wilkinson CR (1993) Coral reefs of the world are facing widespread devastation: can we prevent this through sustainable management practices? Proc 7th Int Coral Reef Symp 1:11-21.