

**SCOR Working Group 104:
Coral Reefs Responses to Global Change: The Role of Adaptation
Report to SCOR General Meeting**

Submitted by R. W. Buddemeier, chair, 30 September 1998

Activities since the previous report may be divided into two major categories.

1. The final symposium was held January 6-7, 1998, as part of the joint annual meeting of the Society for Integrative and Comparative Biology (SICB) and its associated societies*, the International Society for Reef Studies (ISRS), and the Ecological Society of America (ESA), held at the Boston Marriott Hotel -- Copley Place, January 3-7, 1998. The symposium, "CORAL REEFS AND ENVIRONMENTAL CHANGE -- ADAPTATION, ACCLIMATION, OR EXTINCTION" featured invited talks by A. B. Pittock, B. N. Opdyke, J. Pandolfi, R. A. Kinzie III, R. Gates, K. Yamazato, B. Carlson, H. Lasker, J. Benzie, D. Potts, Rowan, R. P. M. Bak, T. Done, R. Karlson, J. Kleypas, T. Done, J.-P. Gattuso, B. Hatcher, S. V. Smith, R. W. Buddemeier, and was accompanied by contributed paper and poster sessions on related themes. The symposium received financial sponsorship from SCOR, SCOR, LOICZ, NOAA, and SICB, and substantial in-kind support from ISRS. A final working group meeting was held immediately following the Symposium to review and integrate the contributions.
2. Communication of results and findings:
 - a. By consensus of the working group, the contents of the symposium were deemed to represent a significant change in the basis for our understanding of the subject, and volunteers agreed to help spread the information. A summary statement (Appendix A of this report) was drafted and subsequently approved after e-mail circulation. This statement was posted on the NOAA-based Coral Reef WWW page, and was used by various members as a basis for reports and announcements that appeared in publications of the AGU, ESA, BES, ISRS, GSA, the Journal of Environmental Conservation, and a variety of other newsletters and releases.
 - b. Proceedings: As planned, the Symposium proceedings will appear as a dedicated, refereed issue of American Zoologist, v. 39 No. 1, in early 1999. Fourteen articles, representing a broad range of the key issues presented at the symposium, have been accepted, and production is on schedule.
 - c. Further publication: A consortium of participants and collaborators has developed a major review article, which is being submitted to a high-visibility journal. Two participants who were unable to contribute to the Proceedings have committed to publish their material as follow-up papers. Various participants have received workshop, speaking, and writing invitations as a direct result of the WG activities to date.

Relevance to Societal Needs: Coral reefs, both in their own right and as a component of coastal zone management, are a focus of intense attention and concern. Although loss of ecosystem function and biodiversity is a major concern, the time constants of reef systems are long compared to most research and management horizons. The integrated, scale-sensitive focus of WG-104 reviews and assessment provides a new, fundamental science, basis for understanding long-term reef dynamics and their interactions with human societies.

Newsletter material: See appendix A; also, copies of various releases, notices, and publications have been forwarded to the Executive Office.

Other Actions: Following the success of the Symposium, all of the participants who were not already members of WG-104 were named associate members in recognition of their contributions (see list at end of Appendix A), as was Dr. Chris Langdon, who presented a key contributed paper and joined with WG members in developing follow-up publications.

Further actions: Members will complete their individual commitments to the publication process, and can be expected to continue with follow-up activities on their own initiatives. The formal commitment and term of WG-104 expires with the issuance of the publication, and no further formal activities are planned or expected.

Budget requests: No further formal budget request is made, consistent with the preceding point. However, it is noted that page charges will be required for the Proceedings. At present it is expected (and/or hoped) that the necessary costs can be met by a combination of individual author contributions and left-over symposium funds. If that proves not to be the case, a special supplemental request might be made. The maximum possible liability is on the order of a few thousand US\$.

Final comments from the Chair, WG-104: On my own behalf, and on behalf of the other members of the Working Group, I wish to thank the Executive Committee, the Executive Officer, staff, and all who have contributed to what we feel has been a very successful endeavor, and one that has been of benefit to both the participants and a much larger community.

I wish to particularly draw attention to the co-sponsorship of LOICZ as a significant factor in the overall success and impact of the efforts, and extend my thanks to the present and former officers and steering committee members who made this possible.

I further suggest that this type of approach – co-sponsorship of working groups or related activities – is one that can very effectively leverage resources, achieve a critical mass of participation and attention, and avoid duplication of efforts. I think this is particularly a factor as SCOR turns more attention to its relevance to societal needs – having an impact beyond the narrowly defined research community requires visibility, outreach, and resources beyond the level of traditional working group activities in the past.

CORAL REEFS AND GLOBAL CHANGE: ADAPTATION, ACCLIMATION OR EXTINCTION? -- INITIAL REPORT OF A SYMPOSIUM AND WORKSHOP

EXECUTIVE SUMMARY

Major revisions of concepts about corals and reef systems were developed by an international working group of scientific experts that met in conjunction with the Society for Integrative and Comparative Biology, the International Society for Reef Studies, and the Ecological Society of America (Boston, January 3-11, 1998) to evaluate the scientific basis for growing concerns about the survival of coral reef ecosystems facing global change and local stresses. The group, sponsored by the Scientific Committee on Oceanic Research (SCOR) and the Land-Ocean Interactions in the Coastal Zone (LOICZ) core project of the International Geosphere-Biosphere Programme (IGBP), and with the support of the NOAA Coastal Ocean Program, produced an interdisciplinary synthesis with important implications for research, assessment, and management. Key conclusions were:

- The calcification rates of corals, coralline algae, and coral-algal communities depend on the calcium carbonate saturation state of surface seawater, and are expected to be reduced by rising atmospheric carbon dioxide. This represents a global, systemic, climate-related threat to the functioning of reef ecosystems that will interact with the more immediate anthropogenic local stresses.
- Coral reefs and communities are products of processes operating over a wide range of interacting time and space scales, with fundamentally different controls operating at different scales. While short-term responses will be controlled by local environmental conditions and biotic responses, the longer-term sustainability of a reef system depends on the recruitment, dispersal, persistence, and interactions of populations at larger scales.
- Corals, and to some extent reef communities, possess numerous mechanisms for acclimatization and adaptation -- diverse reproductive strategies, flexible symbiotic relationships, physiological acclimatization, habitat tolerance, and a range of community interactions. However, current understanding of these mechanisms, as well as of the critically important calcification mechanisms, is inadequate to explain the past success of corals and reefs or to ensure their conservation for the future.

Unlike many terrestrial ecosystems, coral reef ecosystems appear to be directly threatened by globally increasing atmospheric CO₂. Therefore, conservation or management strategies aimed at removing or mitigating only local, human-derived, or recently applied environmental stresses are likely to be inadequate. Corals and reefs are potentially robust and resilient, but realizing that potential requires the development of new approaches and greater integration of fundamental and applied research, conservation, and management.

SYMPOSIUM AND WORKSHOP OVERVIEW

INTRODUCTION

CORAL REEFS AND GLOBAL CHANGE: ADAPTATION, ACCLIMATION OR EXTINCTION? was the theme of a symposium and integrating workshop held in Boston, January 3-11, 1998, in conjunction with joint meetings of the Society for Integrative and Comparative Biology (SICB), the International Society for Reef Studies (ISRS), and the Ecological Society of America (ESA). The focus of the symposium and the subsequent workshop was on reports of Working Group 104 of the Scientific Committee on Oceanic Research (SCOR), co-sponsored by the Land-Ocean Interactions in the Coastal Zone (LOICZ) core project of the International Geosphere-Biosphere Programme (IGBP) and with the support of the NOAA Coastal Ocean Program. The reports of Working Group 104 members and invited contributors formed the basis for discussions.

This working group has been studying the topic "Coral reef responses to global change: the role of adaptation" for nearly four years, and the symposium provided opportunities to augment its findings with contributed and invited papers from other experts, to benefit from public review and discussion, and to integrate the output in a workshop. Proceedings will be published in a forthcoming issue of American Zoologist.

Both the symposium and the working group focused interactions within a highly interdisciplinary group -- biogeochemists, geologists, paleobiologists, climatologists, aquarists, geneticists, and organismal, ecological, and evolutionary biologists -- on the diverse lines of evidence concerning corals, reefs, and their responses to environmental change. The variety of expertise, the specific nature but global scale of the topic, and the opportunity to develop conclusions over time all contributed to the emergence of fundamentally new views of the nature and functioning of 'coral reef systems' that will have major implications for future research and management.

The conclusions below are based on major points of the Symposium and contributed papers, augmented by subsequent discussions and then integrated and interpreted during a post-meeting workshop. Although interdependent, they are presented under topical categories for convenience.

CLIMATE AND GLOBAL FORCING

One unique feature of the Symposium was a review of the general status of global climate change knowledge from a coral reef perspective, including results of a major regional climate-change modeling effort directed toward tropical marine environments. The focus of symposium and working group was on the biotic effects of climate, but review and analysis indicate the importance of carbon-cycle feedback. Coral reefs depend on calcification for production of the reef structure, but marine calcification is a net source of atmospheric CO₂, not a sink. The effects

of coral reef and other calcifying communities on the global carbon cycle may be significant in the long term, but are very minor compared to present anthropogenic CO₂ emissions. However, direct effects of changes in atmospheric CO₂ on coral reef communities may be as great as or greater than the effects of climate change. The key coral and reef-related global climate and geochemistry points were:

- Despite the Kyoto protocol, atmospheric CO₂ will continue to increase beyond 2100; it is projected to reach two times the preindustrial level of about 270 ppm by the year 2070, and approximately 700 ppm by 2100. These atmospheric changes will cause significant changes in the carbon chemistry of surface ocean water, especially decreases in pH and carbonate ion concentration, which will reduce the calcium carbonate saturation state.
- Translation of the expected global warming (about 2 degrees C by 2100) into regional sea-surface temperature (SST) is difficult because of uncertainty about the physical controls on tropical SST, but probable outcomes include: (1) poleward movement of the isotherms currently associated with coral reef distributions; (2) some rise in mean SST within the present tropical-subtropical latitude ranges; and (3) some degradation of coral communities by local-to-regional episodes of higher temperature within the present warm-water zones.
- Projected rates of sea-level rise (15-95 centimeters by 2100) are well within geologic ranges and measurements of accretion rates for unstressed reefs. However, interactions among decreased calcification rates and other stresses (discussed below) may diminish the ability of reefs to keep up with rising sea level.
- Widespread increases in riverine flood frequency and magnitude will produce a greater incidence of high turbidity, nutrient loading, and other pollution episodes in coastal reef environments.
- There will be possibly significant changes in ENSO and tropical cyclone climatology. Tropical cyclones may increase 10-20% in intensity by 2070, with a possible poleward extension of storm tracks. Effects on reefs of these changes in climatic stress, especially extreme events, will vary regionally.

REEF PERSISTENCE -- PAST, PRESENT, AND FUTURE

Four earlier glacial periods over more than a billion years of earth history ended with mass extinctions of reef organisms, prolonged periods without reefs, and the eventual evolution of very different reef assemblages. These events may provide very general models for the potential effects of climate change on modern coral reefs. However, such comparisons must be tempered by the long time scales of these past events, and by understanding of the characteristics of the scleractinian corals that are the modern reef-builders. Within the Quaternary history of the earth, contemporary levels of anthropogenic stress are unique, and CO₂ concentration, temperature, and sea level are all at or near past maxima -- and projected to rise still further. The question of whether cumulative effects of human impacts have the potential to accelerate major changes in

such processes, on global evolutionary as well as on local ecological scales, was addressed by considering aspects of coral reef history and science relevant to reef persistence.

- While the distinctions among corals, coral communities, living coral reefs, and coral reef systems (or ecosystems) are both real and important, these categories are often confused. Their fates are intimately interconnected, but they are not the same, and an uncritical focus on 'coral reefs' may ignore vital aspects of the various interacting components that form coral reef ecosystems.
 - Many reefal species also exist beyond the range of reefs and/or within non-reefal communities, where they may play important roles in preserving the resilience of reefal systems
 - Both evidence and inference suggest that coral reefs (as accreting coral communities living on calcium carbonate accumulations 'of their own construction') are not only difficult to define, but are also more vulnerable and more episodic in both space and time than are their component species and assemblages.
- There is empirical evidence, at all scales and from a wide range of sources (geological and biological; field, laboratory and aquarium; theoretical and experimental), that corals as a group of organisms possess a wide range of adaptive and acclimative mechanisms, and that most of these mechanisms appear relatively robust and/or resilient in the face of stress. Coral community structure is dynamic on scales of years to centuries, and this dynamism may provide long-term resilience (or 'community adaptation') in response to stresses, including global environmental change. However, the unprecedented variety and magnitudes of chronic anthropogenic alterations of modern reef environments may undermine this resilience.

COMMUNITY AND POPULATION DYNAMICS

Consideration of global and large-scale regional distributions of reef organisms, populations, coral reef systems, and environmental variables yielded the following conclusions, some of which represent substantially new or different perspectives on corals and reefs. Some key points are described in terms of 'metapopulations,' which may be thought of as sets of spatially separated sub-populations linked by dispersal, or more simply as "populations of populations."

- Distributions of reefs (certainly) and coral communities (probably) are correlated not only with sea-surface temperature, but also with available light and with calcium carbonate saturation state. Independent studies indicate that these additional variables may be important controls over coral and reef function and distribution. This is a significant change to the traditional view that temperature is the primary control on reef biogeography.
- Limits of distribution and abundance of reefal species are not necessarily determined by the same processes that determine limits for reefs and reefal communities. Modern distribution patterns, as well as the ability of reefal species to adjust distributions in the face of climate change, can be modelled using metapopulation models in which patterns of abundance and

distribution are functions of local population dynamics. These dynamics in turn determine persistence and dispersal, which controls the origination of populations. Both local population dynamics and patterns of dispersal are sensitive to past and future climate change.

- Ecological, genetic, and species diversities reflect history, including consequences of changes in patterns of dispersal within metapopulations..
 - Patterns determined during periods of intense disruption (e.g., low sea-level stands) may persist over temporal scales much longer than needed for their establishment, and may persist beyond subsequent disruptions.
 - Regional patterns also reflect persistent barriers to effective gene flow and dispersal over larger temporal and spatial scales; these barriers may constrain the development of reefs.
 - Regions with extreme isolation of reef communities, restricted gene flow, limited dispersal, and few refugia will be most vulnerable to major changes and least likely to respond resiliently, especially in geographically or ecologically marginal areas.

RESPONSES AND REACTIONS

Because coral reef 'systems' interact with each other and with global climate across a wide range of time and space scales, there are some fundamental limits on predictability. However general predictions can be made about the effects of global or large scale processes at scales of years to centuries.

- Calcification of reef corals, coralline algae, and coral-algal communities is sensitive to the calcium carbonate saturation state of the water. While this is consistent with studies of foraminifera, geochemical expectations, and geological/paleontological evidence, it has not previously been recognized as a major factor in coral/reef biology.
 - There was consensus that the greatest global climate-related threat to corals and reef systems is the very real possibility that increased CO₂ will cause reduced rates of calcification.
 - Some, but not all, participants felt that a rough estimate of the magnitude of this effect was possible; and that an overall 10-20% decrease in reef-related calcification may follow from the projected doubling of preindustrial CO₂ levels within the coming century.
- Mechanistic understanding of acclimatization and adaptation by corals is extremely limited.
 - Understanding of acclimative mechanisms is largely confined to photosynthetic responses to environmental irradiance.
 - In contrast, little is known about the cellular and biochemical pathways of acclimatization/adaptation to temperature change and other environmental variations, although recent studies of the symbiotic associations that sustain corals reveal that complexity and flexibility in host-symbiont partnerships may provide important and rapid mechanisms of acclimatization/adaptation to environmental change.
 - More importantly, because the mechanisms of coral calcification and their interactions with the photosynthesis of the symbiotic algae are largely unknown, corals' abilities to acclimatize or adapt to changes in seawater chemistry resulting from global increases in atmospheric CO₂ cannot be predicted.

- Lack of knowledge about the ranges of reproductive behavior and their environmental relationships limits understanding not only of dispersal and recruitment, but also of whether hybridization and somatic mutation are critical adaptive mechanisms.
- Sensitivity to saturation state, in conjunction with other influences operating over various scales, means that global climate-related change will apply significant stresses to coral reef systems.
 - This finding DOES NOT alter the assessment that the primary threat to reefs and coral communities is local and regional anthropogenic stresses, often of a chronic nature.
 - This finding DOES substantially alter the previously common view that the effects of global climate change are negligible, or indeed potentially positive, compared to local threats. Instead, global-scale changes are expected to significantly and progressively increase the vulnerability of many reefs to both acute and chronic local stresses.
- Resilience and/or robustness of modern assemblages may be "lost" as environmental changes exceed the adaptive and acclimative capacities established under previous rates and ranges of disturbance.
 - Globally, the issue of greatest concern is atmospheric CO₂, which is projected to exceed the estimated maxima for the Quaternary period during the coming century. This will both cause and interact with temperatures that also approach the maxima experienced by reef organisms over the past several million years.
 - Local and regional anthropogenic stresses are unprecedented in distribution, magnitude, rate of change, and, in some cases, nature. These will interact synergistically not only with each other, but also with global climate-related factors.

IMPLICATIONS

These findings and observations, resulting from focused interdisciplinary review and interpretation of many lines of evidence addressing corals and reefs, provide perspectives different from those obtained from discipline-based or local studies. The picture of coral reef ecosystem responses to the effects of global increases in CO₂ is fundamentally different from that of terrestrial ecosystems, for which it is widely accepted that increased primary productivity is advantageous. In contrast, the dominant global trend for coral reefs, a reduction in calcification, is fundamentally unfavorable for coral reef systems.

Widespread observations of intrinsic resilience and robustness in corals and reefs suggest that they need not necessarily disappear as a result of accumulating stresses. However, the recognition that global factors are likely to increase reef vulnerability to currently dominant anthropogenic stresses adds urgency, as well as new perspectives, to the need to develop new management, protection, and conservation measures on relevant spatial and temporal scales. Long-standing lack of knowledge about the mechanisms of calcification, the nature of symbioses, the physiology of acclimatization, reproductive biology (ranging from taxonomic and geographic inventories of behavior and success to mechanisms of adaptation), the nature and extent of biodiversity, and the long-term ecological structures and dynamics of coral reef communities

hinder our ability to make decisions and useful predictions that address the issues raised by our rapidly developing understanding of large-scale processes. These uncertainties point toward research needs that will concurrently address both fundamental and applied problems.

Individual corals, communities, and living reefs are controlled by fundamental interactions among many environmental variables and biotic responses at local scales; this limits detailed or quantitative predictions in most situations. In addition, living reef communities are products of complex and dynamic interactions at all scales -- from dynamic, multicomponent symbiotic variations on scales of days or weeks, to gene flow involving metapopulations at millennial time scales. These are significant external factors determining the responses of individual reefs and communities to local conditions, and their probabilities of future change.

CONCLUSIONS

The Working Group's findings indicate the need for significant revision of our research, assessment, and management approaches to coral reef problems. Key issues include:

- Calcium carbonate saturation state is potentially the most important control on calcification by reef organisms and communities. Increasing atmospheric CO₂ levels therefore represent a global and increasing threat to coral reef systems. This significantly changes our assessment of the importance of global climate change issues in contributing to reef system stresses.
- Coral reef systems are the results of interacting processes and constraints operating at a variety of time and space scales, whereas the study, management, and protection of reef ecosystems are intrinsically local and regional enterprises operating on human time scales. Effective local action must be informed by global understanding of controlling responses and interactions at a variety of scales -- simply reducing or mitigating local stresses may not be adequate to insure reef sustainability in the presence of large-scale constraints or systemic deterioration, and in the absence of mechanistic understanding.
- Corals, and to some extent reef communities, possess diverse and impressive arrays of acclimative and adaptive mechanisms -- reproductive strategies, flexible symbiotic relationships, physiological acclimatization, habitat tolerance, and a range of community interactions. However, inadequate understanding of these phenomena, and of the critically important calcification mechanisms, severely limits our ability to predict and manage the future of reef systems.
- Local anthropogenic threats remain the most immediate threat to coral reef systems, but responses to local stresses are now seen as being substantially conditioned by global environmental changes and by biological patterns and distributions established over much larger time and space scales. Consideration of the biological effects of reduced calcification and other stresses indicates that other environmental changes affecting tissue growth and metabolism, calcification, or demography (reproduction, recruitment, survival) of corals are all likely to reduce further the capacity of reef communities to maintain themselves, and increase

the probabilities that thresholds to major disruptions -- such as ecosystem collapse or organism extinctions -- will be exceeded.

Symposium Participants:

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(WG-104 chair; Symposium co-organizer)

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