

Coral Adaptation and Acclimatization: A Most Ingenious Paradox¹

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SYNOPSIS. Reef corals and the communities they form evidently possess effective mechanisms of adaptation and acclimation that have ensured their survival and recurrence over geologic time. Current reef degradation suggests that these mechanisms are being taxed beyond their limits; understanding of the problem is hampered by serious inadequacies in our understanding of physiological stress responses, the range and implications of reproductive strategies, and the mechanisms of calcification and algal symbiosis. Reef community and population responses to environmental change appear substantially different on different time scales, and a combination of short-term perspectives and definitional confusion complicates interpretation and prediction of reef responses. Calcium carbonate saturation state is now recognized as a potentially important control of reef calcification, which means that rising atmospheric CO₂ represents a direct threat to reef ecosystems on a global scale.

INTRODUCTION

“A paradox, a paradox,
a most ingenious paradox!”
(W. S. Gilbert, “The Pirates of Penzance”)

Coral reefs are one of the few marine ecosystems that might be described as “charismatic.” Their diversity, complexity, and visual beauty engage the interest of the lay public; their roles as resources in coastal morphology, productivity, and economics attract the attention of planners and managers, and their unique suite of biological processes, geological features, and climatic indicators assures the continued attention of scientists.

It is not surprising that the same characteristics that make coral reefs interesting and accessible to tourists as well as scientists—their obligate occupancy of shallow, warm, clear-water benthic habitats—should make them vulnerable to human environmental alteration of the coastal zone. Nor is the upwelling of concern about threats to, and the decline of, reefs surprising. What is surprising is our lack of understanding of

the mechanisms of stress response and recovery at both organism and community levels, and our difficulties in matching observed behavior on organismic and community (both reef and human) time scales with evidence from the geologic and evolutionary records.

Recognition of the importance of these subjects led to the establishment of Working Group 104 (Coral Reef Responses to Climate Change: The Role of Adaptation) by the Scientific Committee on Oceanic Research (<http://www.jhu.edu/~scor/>) in 1994. It was subsequently co-sponsored by the Land-Ocean Interactions in the Coastal Zone {LOICZ—<http://www.nioz.nl/loicz>} program element of the International Geosphere-Biosphere Programme. The objective, simply stated, was to resolve the “most ingenious paradox” of organisms that appeared biologically fragile but geologically robust. This symposium was the product of the working group, and one that went well beyond the review-describe-recommend mode of operation common to many committees. Among the papers published here are major revisions of conventional wisdom, challenges to standard assumptions and research practices, new insights, and approaches to common questions from a variety of scales and perspectives that bring them into a sharper focus.

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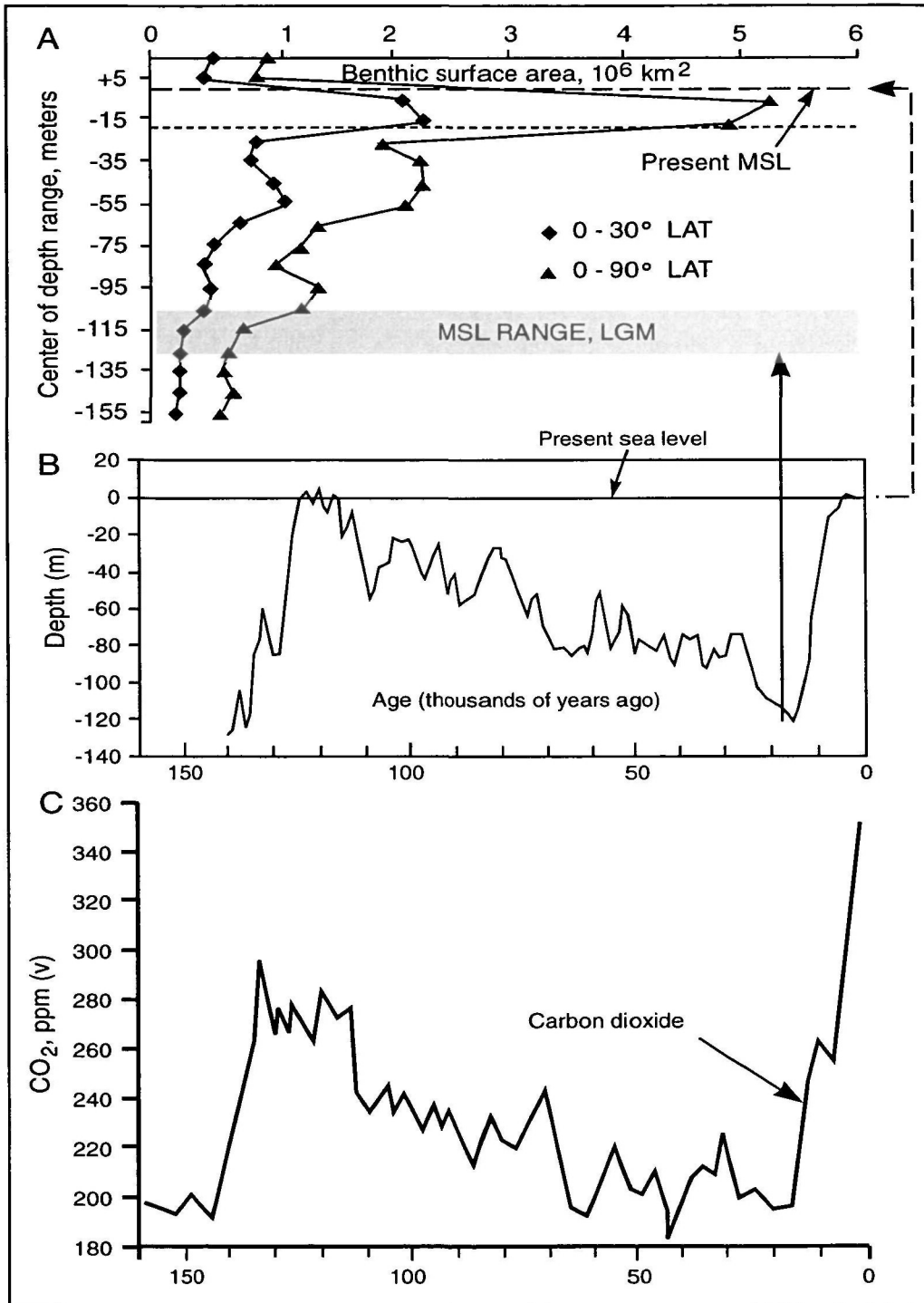


FIG. 1. A. Estimates of benthic surface as a function of depth (relative to present mean sea level, MSL) derived from the ETOPO5 data set. Totals are presented for the whole earth, and for the latitude band of coral reef occurrence (30°N–30°S). B. Late Pleistocene sea level history, adapted from Chappell *et al.* (1996). At the Last

GLOBAL CHANGE AND THE BIOGEOPARADOX

Reef structures containing, and often dominated by, scleractinian corals have occurred for over 200 million years (Veron, 1995). Through extinctions, hiatuses, and climatic oscillations, reef-building corals and the impressive biogeomorphic structures they create have reappeared over and over. On geologic scales ranging from tens of millions to tens of thousands of years, they appear to be hardy survivors and persistent or recurrent features. At the time scale of Quaternary climatic oscillations, Figure 1 illustrates some of these features. A scant 10–20 kyr ago, lowered sea level meant that the benthic area available for reef development was almost a factor of 10 less than at present—even without allowance for compression of the tropical climatic zones. We see at the recent end of the CO₂ (Fig. 1C) curve the dramatic rise beyond the normal range due to human intervention. Added to these factors is the ongoing revision of our views on tropical temperatures at glacial maxima—recent model results suggest that tropical sea surface temperatures were 3–4°C lower at the Last Glacial Maximum (LGM) (Ganapolski *et al.*, 1998), and field studies find evidence for decreases of up to 6°C (Beck *et al.*, 1992; Guilderson, *et al.*, 1994). Changes of this magnitude would place all or most reef areas below what is currently regarded as the optimum temperature range for coral growth. All in all, both the fossil record and climatic history suggest that “coral reefs,” *as we know them*, are geologically rare features which happen to be unusually abundant now.

This picture of robustness or resilience in the face of ubiquitous stress and environmental change is in contrast to our present-day, short-term experience and biological observations. Biologists have tended to view reef ecosystems as precariously balanced on a web of environmental controls—light, temperature, salinity, nutrients,

water movement, etc.—any one of which could bring the system down if changed. Predictions of reef degradation and loss that seemed extreme less than a decade ago (Wilkinson, 1993) now look far more realistic in the wake of systematic assessment (Bryant *et al.*, 1998). The local and regional anthropogenic components of Global Change seem to be providing an effective, if unplanned and uncontrolled, experimental verification of those pessimistic predictions.

The term “Global Change” has been used in two ways: to mean “climate change,” with emphasis on temperature, rise in sea level, etc. responses to changing greenhouse gases (especially CO₂); and also as a more anthropocentric term addressing change from a social science perspective. The usages have gradually merged, and the more natural-science use of the term has evolved to include “secondary variables” such as changing runoff, oceanic CaCO₃ saturation, etc., and also “non-climate variables” such as human forcing of nutrients and other pollutants on a global scale.

Related terms that have been used include **systemic** changes throughout any compartment of the Earth System (*e.g.*, temperature rise, atmospheric CO₂ rise), and **cumulative** changes at discrete locations, but combined to have global importance (*e.g.*, human population pressure, eutrophication, altered runoff). A further important development with respect to discussions surrounding global change is the recognition that many of manifestations of global change will be or already are being felt most strongly in the coastal zone, a region of high gradients and variability (Smith and Buddemeier, 1992). There has also been recognition of inferential value derived from the reconstruction of past changes, as recorded in geological record, and the recognition that coral reefs are particularly good records of past change.

The paper by Pittock (1999) is a novel

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Glacial Maximum (LGM), benthic surface area (arrow to 1A) in the depth range of primary reef growth (taken as 0–20 m, but the relative change is insensitive to the exact values used) was reduced by a factor of 5–10 relative to present. C. History of atmospheric CO₂ concentrations deduced from ice core samples and other data.

contribution to the coral reef literature in representing an examination by a global-change climatologist of the prospects for change in the regions, variables, and processes that are of specific relevance to coral reef systems. This discussion highlights the potential for synergism among stresses, such as the potential for interactions among reduced calcification rates due to CO₂ increase, rising sea level, and increased sea surface temperature. It also addresses the critical issue of threshold effects, which are discussed from a paleobiological perspective by Pandolfi (1999). Gattuso *et al.* (1999) focus on the CO₂ issue and review present knowledge of the effect of aragonite saturation state on photosynthetic and calcifying organisms and communities. They estimate that the depression of surface ocean supersaturation levels by rising atmospheric CO₂ may have reduced global reef calcification by 10% between 1880 and 1990, and may cause an additional decrease of 22% between 1990 and 2100.

Even though reviews of the problems facing coral reefs have consistently emphasized that local and regional anthropogenic impacts are a far greater immediate threat to coral reefs than Greenhouse-enhanced climate change (Brown and Ogden, 1993; Glynn, 1991), interest in the response of corals and reefs to climate change remains high. There are several reasons for this. One is the increasing recognition that the various components of "global change" are synergistic and not easily disentangled into tidy causes and effects; another is that we are unsure whether there may be a climate-change component underlying some of the very large-scale, otherwise unexplained phenomena such as wide-spread, high-temperature-related bleaching (Brown and Ogden, 1993; Glynn, 1991), and the collapse of coral populations in the Caribbean region (Jackson, 1997). Conservation or restoration efforts may be misdirected if the natural environment is itself a moving target. And finally, adaptation, acclimation, and acclimatization (used in the sense defined by Gates and Edmunds [1999]) in organisms unquestionably exist, and the mechanisms that have been shaped by past climatic variations may be critical to the sur-

vival and distribution of corals and communities facing novel combinations of stresses. The paper by Carlson (1999) demonstrates that the plasticity and range of organism acclimatization to altered environments extends far beyond what we normally observe in nature. Aquarium specimens appear to thrive in environments vastly different from their natural habitats, albeit with grossly altered forms and behaviors.

PROBLEMS, CONCEPTUAL AND DEFINITIONAL

Consider the original definition of coral reefs: Coral reefs are rocky structures in the tropics. Ships can run into these structures and do great damage to themselves. Historically, the definition of reefs has shifted from "structures shallower than 30 feet" to "structures shallower than 60 feet," because of the greater draft of modern ships. To be called **coral** reefs, these hard, rocky structures have hard, rocky (coralline) animals and plants living on them. The term "coralline," in this context, refers to organisms that deposit a calcareous skeleton. Thus the original concept of reefs stemmed from how sailors visualized these features.

The definition was modified by geologists to recognize that most material in a coral reef is not contributed by framework builders (yet framework is the part that defines reefs to a mariner!). Both biologists and geologists working on reefs tend to expand or contract what they are willing to call "the reef" to meet their scientific interests. Fishermen, tourists, or other "users" of reefs similarly modify the definition.

From a large-ecosystem perspective, a useful general scientific definition might be something like this: "Coral reefs are shallow-water, tropical or subtropical marine ecosystems that contain one or more communities dominated by corals and other framework-building organisms such as crustose coralline algae. Communities of framework-building organisms have persisted or recurred over a sufficiently long period to have built a three-dimensional structure on top of the underlying (non-reef) substrata."

Within the limits of this definition, parts of coral reefs are likely to be visually char-

acterized by corals, but many biotic communities with corals are not either reefs or even reef communities, because they fail to create a three-dimensional structure. Many (perhaps most) reef-associated communities have few or no corals. Examples include seagrass beds, algal communities, and soft-sediment communities. Even the plankton community within the confines of a coral reef is part of the ecosystem definition.

A recent study of “coral reef area” (Spalding and Grenfell, 1997) illustrates the wide range of values that can be associated with different definitions of the same term. The issue is important, since the total area of non-reef communities containing corals or other biota commonly associated with reefs (*e.g.*, crustose coralline algae) is likely greatly to exceed the area of “coral reefs,” and most calcification (and other metabolism) by “reef biota”—even in this era of unusually abundant reefs—probably does not occur on reefs! This point, taken together with the reef abundance implications of Figure 1, suggests that non-reef areas with coral reef organisms may be a key to the survival of coral reef biota through geological time.

The relationship of the living community to the presence or absence of an underlying carbonate structure is a persistent problem in reef studies because of the disparate time scales involved. Maximum reef carbonate accumulation rates are on the order of a cm/yr (Buddemeier and Smith, 1988; Opdyke and Wilkinson, 1993), so a perceptible reef structure typically represents at least several centuries of accumulation. The observation of Done (1999) that “coral reef communities” undergo repetitive destruction and replacement on time scales of decades means that any living reef community may have no more in common with its predecessors that formed the reef than a preference for elevated, hard substrate. A focus on the navigational hazard rather than the living community—as seen in the modern assumption that “coral reefs” are special and distinct from “coral communities”—artificially compartmentalizes the system and inhibits understanding.

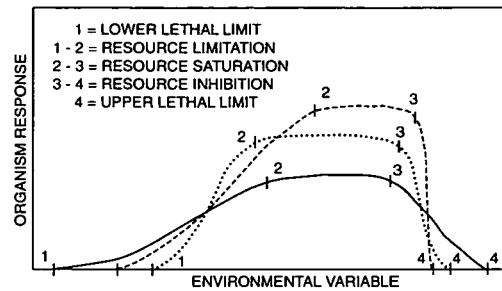


FIG. 2. Possible trajectories of organism responses to changes in environmental variables. The approximate coincidence of endpoints and plateaux is for illustrative convenience; real response curves will show much greater variations and offsets.

RESPONSES TO ENVIRONMENTAL CHANGE

Single-variable responses

Figure 2 illustrates typical patterns of organism response to environmental change. The response curves could apply equally to “resources” (*e.g.*, food, light, nutrients) that are consumed in some way, or to environmental “factors” (*e.g.*, temperature, pH, etc.) that are present but not consumed; the term ‘resource’ is used loosely in the figure. The three curves might represent responses to the same variable by different organisms, responses to different variables by the same organism—or even the responses to the same variable of the same organism after different acclimatization experiences. Point 1 represents the lower lethal limit (or survival threshold); the interval between points 1 and 2 is the region of resource limitation (or, from a more optimistic viewpoint, “resource stimulation”), where there is a positive organism response to an increase in concentration or intensity; the range between 2 and 3 represents resource saturation (little or no response to change); the shape of the curve between 3 and 4 depicts resource inhibition (negative organism response to further increase); and 4 is the upper lethal limit.

Responses discussed in this symposium vary widely among organisms and communities. For example, Kleypas *et al.* (1999) show with statistical analyses of biogeographic data that naturally occurring sea-surface temperatures can be too high or too low for the growth of coral reef com-

munities (*i.e.*, the full range of limitation, saturation, and inhibition behaviors in Fig. 2), which agrees with field and laboratory observations at the organism level. However, their analysis shows no evidence of community inhibition by light, although photoinhibition of organism-level photosynthesis can occur when ambient light levels are changed abruptly and there is evidence for subsurface maxima in reef diversity and some coral growth rates (Huston, 1985). The community-level global models of Kleypas *et al.* (1999) agree with the organism and community-level studies reviewed by Gattuso *et al.* (1999) which suggest that aragonite saturation state can provoke resource limitation and saturation responses, but that apparently achievable levels of supersaturation do not inhibit calcification. This not only adds a generally unrecognized variable to the list of “reef controllers,” but it also provides a direct, non-climatic link between reef responses and the rising levels of atmospheric CO₂ associated with global change (Pittock, 1999).

Multiple-variable responses

Neither organisms nor communities respond to their environments with linear combinations of single-variable responses. Rather, there exists some sort of environmental hyperspace where interacting variables create n-dimensional “volumes” of acceptable and optimal conditions in terms of organism response. As long as all or most environmental parameters are well within the optimal central region of the space, considerable resilience, and even actual compensation, may be exhibited. For example, the elevated carbonate saturation states associated with lower CO₂ at the LGM (Fig. 1) may have helped to compensate for the suboptimal temperatures and reduced substrate at that time.

This helps us to understand the subtle character of thresholds (Pittock, 1999; Pandolfi, 1999) in coral and reef responses to environmental change. A major change in one parameter, or a combination of smaller changes in multiple parameters, may leave a community viable and even apparently thriving, but with its volume of optimal hyperspace so reduced that any further chang-

es will almost surely push it outside of its range of tolerances. This view is consistent with the complex problem of defining and identifying ‘turn-offs’ (Buddemeier and Hopley, 1988), and with the long time constants of reef system change and response at regional scales (Jackson, 1997). It also suggests that by the time we perceive a problem on human scales, it may be far too late to address, or even identify, the “ultimate” causes.

Gates and Edmunds (1999) address the issue of acclimatization and stress response at the organism level. Although the lack of specific knowledge about reef biota is depressing, their arguments for the consistent role of protein metabolism and (where appropriate) changes in the symbiotic relationships (*e.g.*, bleaching) provide a glimpse of consistency and of research themes that is echoed by the discussions of Kinzie (1999) at larger scales. He also addresses the potential significance of multi-taxon algal symbioses at evolutionary scales, and stresses the importance—and our regrettable ignorance—of the sometimes Byzantine complex of reproductive strategies available to many corals.

ECOLOGICAL PATTERNS PAST AND PRESENT

Issues of reproduction and recruitment, and of scale, are prominent integrating features of the discussions of community characteristics and distributions. Lasker and Coffroth (1999) address the important issue of clonality and vegetative reproduction as a factor in response to environmental change and how time scale affects that response, filling in one of the gaps in the overall knowledge of reproductive strategies addressed by Kinzie (1999). Bak and Meesters (1999) use demographic data to suggest that shifts in population age distributions may be an indicative result of environmental stress, acting through the medium of recruitment and age-specific mortality.

The analysis of Karlson and Cornell (1999), showing a substantial degree of “openness” in community recruitment patterns, seems consistent with the observations of Done (1999) that local reef community types exhibit a relatively high rate

of turnover. Both of these might appear to conflict with the paleobiological findings of Pandolfi (1999) that indicate a recurrent consistency of composition in Pleistocene reef communities. However, this discrepancy is more apparent than real because of the time and space scales involved, and, in fact, points out important avenues for research. Karlson and Cornell examined species richness (number of species) in local communities across a range of differentially rich regions, whereas Pandolfi examined species composition over long time periods at a few sites in one (species-rich) region. Done, and Karlson and Cornell, used "real-time" data that address scales of decades at most, whereas the paleontological sampling cannot readily resolve time intervals smaller than a few centuries. Are population and ecosystem responses, as we currently define them, intrinsically different as a function of spatial scale? Does turnover and open exchange at decadal time scales "average out" in century-scale integrated samplings, with the "average" signal replicating itself at time scales of 10^3 – 10^4 years? If so, there are some important lessons to be learned at the interface of long-term biology and short-term geology.

Benzie (1999) addresses population patterns at oceanic spatial scales and time scales of 10^5 – 10^6 years; longer than those of Pandolfi's (1999) Pacific study, but comparable in both scale and implications to his present and earlier discussions of species distributions and extinctions. Based on genetic data for coral reef (but not specifically coral) organisms, Benzie shows that pattern is manifest, and that the patterns do not correspond to either traditional interpretations (*e.g.*, of the Indo-Pacific center of diversity as a source rather than a sink), or to contemporary oceanic circulation patterns. This long-term view provides quantifying examples of some of the evolutionary and biogeographic issues addressed by Kinzie, and reinforces the conclusion derived from records over 10^4 – 10^5 years (Fig. 1)—we live, and observe reefs, in an environment that is atypical in terms of the history of corals and reefs, and which is becoming more so as a result of human activity.

CONCLUSIONS

In science, as in comic opera, paradoxes are more often ingenuous than ingenious. The paradox of the epigraph was the question of how the hero, "a youth of twenty summers," could have celebrated only five birthdays. Of course he was born on Leap Day, and an excessive preoccupation with precision and resolution at the daily scale blinded the *dramatis personae* to biological reality at annual and decadal scales.

The major outcomes of the deliberations of Working Group 104 and of this symposium may be summarized as follows:

1. There is a strong suggestion that both coral reef organisms and communities exhibit acclimative and "adaptive" behaviors and considerable flexibility of response to environmental change, at time scales of years to decades. Better understanding of these mechanisms and their limitations would offer some hope for the possibility of conservation and effective environmental management.

2. At various time scales $\geq 10^2$ years, patterns, consistency, and possible constraints become more evident. While some of these may be artifacts of our observational limitations, there is a strong suggestion that there are time and space scales that ultimately constrain the nature of local to regional reef responses.

3. The past several thousand years, and especially the past few decades of relatively intensive scientific study of reefs, are environmentally atypical in terms of long-term reef community and organism habitats. This observation combines with point 2 to suggest that we may be now observing the effects of environmental response thresholds that were crossed long ago in human, but not in reef ecosystem, time scales.

4. Research and conservation efforts focused on narrowly-defined communities or 'coral reefs' are ill-advised; it is almost certainly the wider range of reef-related communities, habitats and organisms that is critical to human understanding and survival of the larger ecosystem.

5. The effect of carbonate saturation state on calcification, and its linkage to atmospheric CO_2 concentration, is now rec-

ognized as a potentially important control on coral and reef community function.

6. Subject to the guidelines and caveats discussed above, the most urgent areas of needed research appear to be:

a. Mechanisms of stress response and acclimatization, both physiological and with respect to algal symbioses.

b. Reproductive strategies of both hosts and algal symbionts and their roles in survival, distribution, adaptation, and evolution.

c. Calcification mechanisms at cellular and organism levels, their environmental controls, and the importance of calcification to organism and community survival under various conditions.

d. Careful integration of paleobiological and paleoenvironmental, as well as real-time, investigations of the above points.

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