Chapter 15. BIOLOGICAL–PHYSICAL INTERACTIONS AND GLOBAL CLIMATE CHANGE: SOME LESSONS FROM EARTH HISTORY

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1. Introduction

Over the last 100 years of the industrial revolution, human civilization has been performing a remarkable experiment on Earth's climate system. Because of a variety of activities related to population growth and economic development, most notably the burning of fossil fuels, humans have increased the concentration of carbon dioxide in the atmosphere by approximately 30%. Carbon dioxide is a greenhouse gas, absorbing long-wave radiation emitted from the planet surface and warming Earth's surface temperature. There is now a consensus that Earth's climate has been influenced discernibly by the increase in CO_2 (e.g., Houghton et al., 1996), although considerable controversy exists over how much the climate will change over the next several centuries as atmospheric CO_2 continues to rise.

The realization that humans are changing Earth's climate is profound, yet it is not the only way in which humans are changing the physical and biological environment. The arrival of humans to the Americas at the end of the last ice age, approximately 14,000 years ago, was accompanied by the extinction of most large mammals, includ-

The Sea, Volume 12, edited by Allan R. Robinson, James J. McCarthy, and Brian J. Rothschild
ISBN 0-471-18901-4

ing mammoths and mastodons, presumably from excessive hunting. Over the last century, human land use has caused an enormous reduction in biodiversity as sensitive ecosystems such as wetlands, tropical rain forests, and coral reefs are encroached or destroyed by human activities. Confronted with these and other impacts of human activities, why is anthropogenic climate change so troubling? One answer is that because the scale of the climate system is so large, the processes that control it so powerful, it seems unimaginable that our climate could be affected by something as subtle as emissons of carbon dioxide. Our climate is heated with light from the sun, modulated by winds driven in part by Earth's rotation, with memory provided by the vast oceans with their deep currents churning the deep at rates hundreds of times faster than that of all the world's rivers combined. The idea that burning a relatively small amount of coal, oil, and gas can affect such a large, complex system, significantly altering its course, forces us to view the relationship between human activities and our planet in a different light.

To scientists who study the oceans, the realization that humans can have a significant effect on ocean temperatures and circulation is equally profound. How can we study the ocean to understand the complex mix of physical, chemical, and biological processes in the context of the perhaps subtle but certainly pervasive effects of human activities? The traditional approach is for oceanographers to make observations and study processes over short time scales, assuming that the system is in some sort of steady state. We presume that we can study short-time-scale processes with characteristic time scales out to several years without consideration of the subtle bias that comes from slow, steady warming due to anthropogenic forcing. But as we begin to explore how the ocean varies not only in space but in time, it becomes important to know whether environmental conditions are changing over the period of our observations and whether our presumption of steady state really applies. For processes such as deep-water formation, which may affect oxygenation of the deep ocean, the problem is even more daunting, as any effects of anthropogenic climate change merely amplify the natural variability that remains poorly described. Moreover, oceanographers are now being challenged to apply their understanding of the oceans and climate to develop some predictive capacity for what changes in the oceans, including all the possible physical, chemical, and biological interactions, we might expect to see over the next century.

2. Scenarios for the Physical Climate System

One approach to studying the oceans in the face of rising greenhouse gas concentrations is to consider specific scenarios for future climatic conditions and then explore how different aspects of the oceans might be affected. A scenario is a coherent, internally consistent, and plausible description of a possible future state of the world. If there were no human influence on the climate system likely to be significant in the near future, scenarios would project a cooling of Earth's climate with an eventual return to a glacial condition. This would be consistent with the orbitally forced climate rhythm of the last million years. Scenarios for Earth's future climate must take into consideration the consequences of changes in radiative forcing attributable to the increases in greenhouse gases that have already occurred, anticipate how these concentrations may change in the future, and attempt to estimate the sign and magnitude of important feedback processes.

The future population of Earth and its consumptive practices will determine rates of greenhouse gas emissions; hence, credible scenarios for future emissions of greenhouse gases must be based on projections of socioeconomic and technological developments. Such emission scenarios can then be used to drive atmosphere–ocean general circulation models (AOGCMs) to allow for the impacts of possible future climates to be evaluated. The most sophisticated emission scenarios are a set of 40 prepared under the auspices of the Intergovernmental Panel on Climate Change (IPCC) in a Special Report on Emission Scenarios (SRES). They are based on an extensive literature assessment, six alternative modeling approaches, and an open process that solicited worldwide participation. These scenarios cover a wide range of demographic, technological, and economic driving forces of future emissions for all relevant greenhouse gases and demonstrate the powerful role of each of these forces on the magnitude of future emissions. Previous scenarios assumed a constant 1% per annum increase in greenhouse gases after 1990. Results from simulations with atmosphere–ocean general circulation models used in IPCC assessments are archived by the IPCC Data Distribution Center. Their climate sensitivity varies; for a doubling of preindustrial CO_2, they yield global mean temperature increases of 2.8 to 5.2°C.

Most models used in the IPCC assessment show weakening of the thermohaline circulation, arising from warmer surface ocean conditions. Results of several studies suggest the possibility that if the rate of change in radiative forcing is large enough and applied for long enough, the thermohaline circulation could collapse entirely. In the models, this typically occurs at four times preindustrial concentrations of CO_2 (Manabe and Stouffer, 1994). The rate of CO_2 increase is now known to be important in determining whether or not a weakening of this circulation ultimately results in its collapse (Stouffer and Manabe, 1999), but the relative roles of heat and freshwater flux in these processes are unresolved. Effects on intermediate water circulation and upper-ocean stratification remain poorly described.

The few models that have sufficient resolution to simulate accurately the air–sea interactions in the tropical Pacific indicate that as Earth warms in response increasing greenhouse gas concentrations, the Pacific climate will tend toward an El Niño condition (Meehl and Washington, 1996; Timmermann et al., 1999). These studies suggest only minor changes in amplitude and/or frequency of interannual variability, but this variability would affect a mean state that is experienced today as a strong El Niño event. The effects of such changes on the biological productivity in the upwelling regions of the eastern Pacific remain largely unexplored.

The disproportionately large increase in temperature evident for the arctic region in all AOGCM climate scenarios forced by increasing greenhouse gas concentrations raises important questions about the effects of climate change on sea ice. Needless to say, were arctic sea ice to be severely diminished or lost altogether, the altered albedo and air–sea fluxes of heat for the Arctic Ocean would profoundly influence northern hemisphere climate. In the nearly three decades of sea ice data now available from satellite passive microwave observations, it is evident that interannual variability is large in both polar regions (Parkinson, 1995). Interannual variability in climate high in the northern hemisphere has several components, such as the North Atlantic Oscillation (NAO) (Hurrell, 1995) and an oscillating regime of wind forcing that links to the NAO (Proshutinksy and Johnson, 1997; Johnson et al., 1999). These are known to be correlated with sea ice extent (Gloersen and Cavalieri, 1986).

Recently, several papers have called attention to the strength of the trend in satellite ice data. Parkinson et al. (1999) analyzed the 1978–1996 period and computed a mean decrease in arctic sea ice extent of −2.8% per decade for this 18-yr period. Johannessen et al. (1999) have further identified a reduction of 14% in the area of wintertime multiyear ice over this same period. Rothrock et al. (1999) carried this analysis further by comparing submarine measurements of arctic ice thickness over the last four decades, and report that thinning is evident at every site sampled, with a mean of −15% per decade. The net effect of the decrease in areal extent and thinning is a loss of 40% of arctic ice volume over the last four decades (Vinnikov et al., 1999).

A lesson from the analysis of sea ice is that the effects of a climate influenced by altered radiative forcing may be prolonged, with their full consequences requiring decades or centuries to materialize. For example, if we assume that the observed loss of arctic sea ice over the last three decades—nearly 40% of its volume—is indeed the result of radiative forcing attributable to anthropogenic greenhouse gases (Vinnikov et al., 1999), even if greenhouse gases were stabilized immediately, melting could continue until there was no multiyear ice in the Arctic Ocean. Another example of prolonged effect is the rise in sea level, which results both from the retreat of alpine glaciers (now documented on all continents) (Warrick et al., 1996) and the thermal expansion of the mass of ocean. The ocean's response to the radiatively forced warming of the atmosphere that is now occurring is relatively slow, due to the high specific heat of water and ocean-mixing time. If, for example, atmospheric concentrations of CO_2 were to be stabilized at 450 ppmv in year 2100, it is estimated that sea level will have risen about 60 cm by the same time. The ocean's volume, however, would continue to expand for centuries under a constant 450 ppmv CO_2, with sea level rising 110 cm by 2200 and 145 cm by 2300, relative to today (Warrick et al., 1996).

3. Incorporating Biology into Climate Scenarios

A concern with all of these climate scenarios involves the many sources of uncertainty inherent in our incomplete knowledge of the ocean–atmosphere system. For example, climate modelers emphasize that feedbacks in the physical climate system, most notably those that involve cloud dynamics, remain a large source of uncertainty in projections of future climate change. In addition, the feedback terms for ocean responses to atmospheric forcing are greatly simplified and almost exclusively physical. They rarely consider biological and chemical responses, including those that involve the carbon cycle. In other words, they assume, naively, that the biogeochemical systems that influence, for example, the rate of sequestration of CO_2 by the ocean, the vertical distribution of carbon, and its residence time in the ocean are of negligible consequence for climate. At the same time, it is difficult to predict how these climate scenarios might affect biogeochemical systems, including ecosystems of all types, without more complete, integrated physical–chemical–biological models of Earth system.

Given the sensitivity of physiological and ecological processes to daily and seasonal cycles in upper ocean mixing and stratification, it is obvious that climate change has profound potential to alter biological–physical interactions in the ocean. One specific concern is with regard to the role such interactions play in the carbon cycle. For example, the amount of carbon stored by the ocean will be affected by changes in the biological–physical interactions, and therefore the magnitude of change in sequestration that could arise with a particular climate scenario is an important research question. The feedback term could be positive or negative, region to region, and hence the global aggregate effect could either exacerbate or ameliorate global climatic change. As described above, emission scenarios now include a range of demographic, socioeconomic, and climate-sensitivity parameters. However, the correspondingly sophisticated climate scenarios for the physical climate system rarely include consideration of the effects of climate change on upper ocean biogeochemical cycles.

The work of Woods and Reid (1993) was one of the first studies to use an upper ocean ecosystem–physical model to examine possible effects of a warmer atmosphere on biological production and ocean carbon storage. Their thesis was that increased radiative forcing would diminish the depth of winter convection and hence reduce the annual supply of nutrients for primary production. A consequence of this would be a weakening of the biological pump, a term promoted by the late Roger Revelle for the biological processes that produce and package organic matter in a form that facilitates its flux to the deep sea via advective/convective mixing or gravitational settling. In the Woods and Reid (1993) model, a diminished export of carbon from the surface ocean resulted in a smaller net flux of CO_2 from the atmosphere to the ocean, and thus a positive feedback to climate, which the authors termed a plankton multiplier effect in global warming scenarios.

Embedding plankton and carbon cycle components in general circulation models is an ambitious task, and only a few efforts have been attempted. Six and Maier-Reimer (1996) were among the first to attain success in the development of a model that reproduces regional differences in seasonal oceanic pCO_2. Maier-Reimer et al. (1996) further modeled the biogeochemical response to changes in ocean circulation and did not see large effects, although their approach did not allow an explicit alteration of the biological activity. Sarmiento et al. (1998) used an AOGCM linked to a carbon model and tested this model's sensitivity to an altered climate. Increased stratification arises largely from the increased temperature at lower latitudes and freshening at higher latitudes from increased precipitation. This very preliminary study calls particular attention to a large potential modification of the ocean's capacity to store carbon in the Southern Ocean. The effect is toward a reduction in ocean sequestration, but they point out that this may be partially offset by enhanced biological production. Although these approaches provide a general sense of bulk changes in the carbon cycle that could occur with future climate change, they are very primitive with respect to their biological components. Changes in upper-ocean stratification will be of profound importance in food web configuration, as questions about which types and sizes of phytoplankton will be favored. This, in turn, will influence the composition of the zooplankton consumers and the efficacy of the biological pump.

4. Observations of Biological–Physical Interactions and Interannual Climate Variability

Clues as to what might be expected in terms of the marine biological consequences of climate change can be found in the observed responses to natural climate variability. There are many relevant results relating patterns in plankton and fish population cycles and climate cycles in the North Atlantic. There are three interannual cycles that are likely to have the largest influence the population dynamics of North Atlantic fish populations. The dominant one is the North Atlantic Oscillation (NAO), which is a multidecadal cycle that is well documented in atmospheric pressure differences between Iceland and the Azores. The NAO has a direct effect on wind patterns over the North Atlantic Ocean. Coincident with maxima in the pressure difference between Ponta Delgada, Azores and Stykkisholmur, Iceland, strong westerlies blow across the North Atlantic and winters in western Greenland are unusually cold. The NAO is characterized by short period fluctuations of about a decade, a dominant two- to three-decade oscillation, and superimposed on these an even longer cycle of particularly intense westerlies, which in the twentieth century had broad maxima at about 1910 and again in the mid-1990s (Houghton et al., 1996). A second climate cycle is the position of the Greenland High, which is correlated with surface ocean currents and with salinity and temperature anomaly patterns. The third is a cycle that reflects more tenuous long-distance links to the El Niño–Southern Oscillation (ENSO). Clearly, the unambiguous attribution of changes in a North Atlantic population to one or another of these climate cycle is difficult. Their interactions will influence the timing and intensity of the cycles themselves, as well as biological responses to them.

5. Lessons from Paleoclimate Data: The Eocene

The general lesson from looking at modern records of biological variability in the ocean is that the biological–physical interactions are so complex that it is difficult to constrain their behavior over cycles of natural variability with only a few cycles of observations. This matter is complicated when one considers the large uncertainty involved with predicting how the physical aspects of climate variability are and will be affected by climate change, quite aside from any biogeochemical interactions. A complementary approach is to look at Earth history for clues to what our future may have in store. This may not solve the fundamental issue of uncertainty about how life will respond to the shifting biological–physical conditions, but at least it can show us how Earth behaved when similar boundary conditions were once imposed.

Most discussion of paleoclimate data within the IPCC has focused on the last million years of periodic glaciations during the Pleistocene epoch, and for good reasons. Observations of climate changes over this time scale are much easier to make, as obtaining the necessary samples usually requires sampling only the upper few meters of ocean sediments. The geologic materials that record these climate changes are much more abundant for the most recent time period as chemical and physical degradation slowly eliminate older materials. The Pleistocene climate records are rich with important lessons about climate change. The dramatic shifts in CO_2 over glacial cycles, as recorded by bubbles trapped in ice from Antarctica (Petit et al., 1999), with coincident changes in biological productivity and marine chemistry (Sigman and Boyle, 2000), have been used to help understand how the carbon cycle might behave in the future. In addition, the rapid, millennial-scale climate changes that punctuate the longer, orbitally driven ice age cycles are relevant to our current predicament, for they are examples of climate changes of similar magnitudes that occur over similar time scales. For example, recent work has shown that during some of these abrupt climate changes, local temperatures in Greenland changed by as much as 10°C over only a few decades (Severinghaus et al., 1998; Severinghaus and Brook, 1999). These observations remind us about instabilities in the ocean–atmosphere system, and the possibility that future changes may not be slow and steady.

The Pleistocene records of climate change do help our efforts to project Earth's climate through the next century, primarily by teaching us what types of behavior in the climate system are possible. However, we must recognize that none of the types of climate variability in the Pleistocene are good analogs for what Earth will experience 100 years from now. The ice core record from Vostok documents that in the last 420,000 years, carbon dioxide levels have never before been above 300 ppmv (Petit et al., 1999). Recent chemical data, including carbon isotopes in organic matter (Pagani et al., 1999) and boron isotopes in sediments (Pearson and Palmer, 2000), suggests that CO_2 was not significantly higher than today at any time in the last 40 million years. The rapid climate changes, including deglaciations associated with rises in CO_2, are stunning examples of abrupt transitions in ocean circulation and climate. But most theories for these rapid changes involve physical instabilities in large ice sheets (e.g., MacAyeal, 1993). This is borne out in the ice core records themselves, for we see such large, abrupt climate shifts only during glacial periods when large ice sheets existed on continents, not during interglacial periods as today.

Fortunately, the geologic record of climate change is far longer than just the last million years. Earth has indeed experienced CO_2 levels comparable to projections for the next century, albeit not for 40 million years. During the Eocene, 55 to 38 million years ago, a sequence of observations supports the view that CO_2 levels were higher than today, probably by four to 10 times modern (e.g., Berner et al., 1983). Evidence abounds that the Eocene climate was warm. Oxygen isotopes in deep-sea sediments indicate that the deep ocean temperature was as high as 12°C (Miller et al., 1987). Fossils of crocodiles that cannot survive cold winters are found in rocks of this age on Greenland (e.g., Marwick, 1998).

Why has a discussion of the Eocene climate been absent from most assessments of future climate change? One reason, aside from the more sparse set of observations discussed above, may be that it is difficult, particularly for scientists who study the modern ocean and atmosphere, to see any similarities between such ancient climate systems and today when so many different boundary conditions have changed, even the locations of the continents and the geometry of ocean basins. The continental configuration in the Eocene was similar to today, with only minor but important differences, including a closed or partially closed Drake Passage between South America and Antarctica, an open Isthmus of Panama, a slightly smaller Atlantic ocean, and an Indian continent just in the process of colliding with Asia. Each of these changes may have had significant effects on ocean circulation and hence climate. This makes it difficult to assess what effects CO_2 might have on the oceans and life when each of the previously mentioned factors, and others not yet identified, may be independent and important agents of change. Nevertheless, the Eocene was the last time Earth experienced CO_2 levels as high as what we expect for the next few centuries, so it seems prudent to look closely and see what we can learn to refine our model projections.

If we group all observations of Eocene climate together, including isotopic, chemical, and paleobiological data, a general picture emerges of a very warm world, with polar temperatures elevated by as much as 6 to 10°C, and tropical temperatures only mildly higher than modern, if at all (Zachos et al., 1994). Some discussion exists of tropical temperatures much colder than today (e.g., Keigwin and Corliss, 1986), leading climate modelers to suggest that some unusual form of ocean heat transport with no additional radiative forcing was responsible for the Eocene climate (Barron, 1987). But more recent analysis of these data sets suggests that a combination of sampling within upwelling regions (Zachos et al., 1994), as well as chemical degradation of the records during burial (Schrag, 1999), accounts for the cold tropical temperatures and that the tropics were likely very similar in temperature to today. In addition to the reduced meridional temperature gradient, there is evidence from the fossil locations of warm-dwelling plants such as palm trees that winters in the continental interiors were much milder than today (Wing and Greenwood, 1993). These general features of Eocene climate are robust, supported by multiple, independent observations, and persist through the peak warmth at about 53 million years ago, and the steady cooling through the end of the Eocene, 15 million years later.

When climate modelers attempt to simulate the Eocene climate (or even earlier greenhouse climates of the Cretaceous) using models designed for the modern, they have difficulty with two main features. First, when CO_2 levels are raised even to four times modern or higher, most models are incapable of producing temperatures at the poles as warm as what the paleoclimate data suggest (e.g., Bush and Philander, 1997). Second, the models are unable to keep the winter temperatures warm at high latitudes, particularly in continental interiors (Sloan et al., 1992; Sloan and Pollard, 1998). These problems with the models are troubling, as they suggest that certain feedbacks may be missing from climate models that may be important as CO_2 levels increase. Sloan et al. (1992) proposed that optically thick polar stratospheric clouds could produce these two features of Eocene climate if the clouds formed at times of higher CO_2. They suggested that the stratospheric clouds were due to oxidation of methane in the stratosphere, increasing the water content in the stratosphere. An alternative view is that these clouds might form as an internal feedback in response to CO_2 alone (Kirk-Davidoff et al., 2000). In either case, the extreme warmth of the Eocene as well as the inability of AOCGMs to simulate that warmth should make us consider whether some important feedbacks are missing from our models that are particularly relevant to higher CO_2 levels that we will experience in the next century.

An important difference between the Eocene and our current climate predicament is that the warm climate in the Eocene persisted for millions of years, with higher CO_2 concentrations brought about most likely from higher rates of volcanic outgassing (e.g., Berner et al., 1983). This means that the entire climate system as well as most ecosystems in the Eocene had time to adjust to the higher radiative forcing and reach a quasiequilibrium state, with no ice caps at high latitudes and very warm deep ocean temperatures. In contrast, our experiment in the coming century represents a warm perturbation to a relatively cold climate. Over the next century, as CO_2 levels continue to rise, there is not enough time (thankfully) to melt all the ice caps or to warm the entire deep ocean. Thus, looking to the Eocene to tell us how ecosystems in the ocean will respond to higher CO_2 has some additional complications. If a major factor in maintaining the warm climate of the Eocene does turn out to be cloud feedbacks, there may indeed be some lessons that are relevant to the next century. However, a better analog may be times in the geologic past when the same type of perturbation in greenhouse gas concentration occurred.

6. Methane Release at the Late Paleocene Thermal Maximum

Just before the Eocene period, at a time now referred to as the Late Paleocene thermal maximum (LPTM), approximately 55 million years ago, there is abundant evidence for a rapid climate change that is in many ways analogous to anthropogenic burning of fossil fuels. Kennett and Stott (1991) first observed large negative excursions in both carbon and oxygen isotopes in the deep-sea sediment record at this time interval, coincident with the largest turnover of benthic foraminifera. Dickens et al. (1995) proposed that the isotope excursions could be explained with an abrupt release of methane from methane hydrates stored in sediments. This methane would add carbon depleted in ^{13}C to the ocean–atmosphere reservoir, causing the excursion on land (Koch et al., 1992) and in the ocean (Zachos et al., 1993). At the same time, the oxidation of huge amounts of methane would cause an abrupt rise in atmospheric CO_2, warming the climate and causing the coincident shift in oxygen isotopes. This hypothesis has since been explored and revised in many different ways, and there are still many uncertainties. For example, it is not clear how much of the methane was oxidized in the ocean and how much was released directly to the atmosphere, stimulating an even more intense climatic response, due to methane's strong greenhouse behavior. In addition, although the timing of the entire isotope excursion is estimated to have taken approximately 200,000 years (Röhl et al., 2000), it remains uncertain how quick was the actual release of methane and buildup of CO_2. However, it is likely that the duration for the release of methane is on the same order as for the anthropogenic release of CO_2 (i.e., centuries) and perhaps even faster.

The LPTM may represent the best natural analog in the geologic record for our anthropogenic experiment with CO_2. Ironically, the IPCC and other assessments of future climate make almost no mention of this event. To be fair, it is possible that the size of the methane hydrate release was far larger than what we are doing, and that any detailed comparison would be inappropriate. On the other hand, the response of sea surface temperatures to the greenhouse perturbation was approximately 4 to 6°C in the surface ocean (Zachos et al., 1993), within the range of predictions by climate models for global temperatures in 2100.

What about the biological response to greenhouse warming? Are there any lessons from the Eocene, or the LPTM (beyond the benthic extinction discussed above), that are relevant to our current predicament? It is important to keep in mind that the discovery of the LPTM is relatively recent and that the scientific community is only now asking such questions. But some insights are available now. One interesting feature of the LPTM with some possible relevance to predicting the ocean's response to future climate change is the extinction of benthic foraminifera. Indeed, more of these single-celled, benthic animals went extinct at the Paleocene–Eocene boundary than at the Cretaceous–Tertiary boundary, when so many other groups of organisms were decimated by a bolide impact (Thomas and Shackleton, 1996). Some have suggested that the extinction of benthic foraminifera represents a widespread anoxic event. If correct, this gives some credibility to what ocean models predict for future climate. An abrupt warming in the surface ocean might cause a temporary stratification of the ocean and a reduction in the thermohaline circulation. In this ocean state, one might expect the bottom waters to drift slowly toward anoxia as supply of oxygenated bottom waters diminished. Thus, one might explain the benthic extinction with an abrupt change in ocean circulation along with a biogeochemical response, quite similar to the idea that anthropogenic warming might trigger a reduction in thermohaline circulation (Manabe and Stouffer, 1994).

An important difference between the Eocene and today is that the mean climate state was already quite warm in those times and had been for tens of millions of years. If we are heading toward such warm conditions, it will be from a relatively cold climate, albeit not as cold as the last glacial maximum. This means that all cold-dwelling plants and animals that currently inhabit the arctic and antarctic, including the many and various aquatic food webs that live in the colder regions of the oceans, had no analog at those times. Imposing a warmer world on these organisms may be cruelest of all, for there may be no region where they can migrate and preserve their current climate adaptation.

7. Coral Reefs and Climate Change

What about plants and animals that live in warmer environments—what does the Eocene or the LPTM tell us about how they will fare in the next century? Shallow-water benthic organisms are among those most likely to be affected by projected future climate change, and corals in particular have been the subject of recent attention. Coral reefs occur in a variety of forms throughout tropical and subtropical seas and account for half of Earth's present production of calcium carbonate (Wood, 1999). The scleractinian corals contain symbiotic algal inclusions within its tissues known as zooxanthallae, which enhance calcification in this dominant group of reef-building corals. While the animal is capable of ingesting nutritious particulate material from seawater, an important component of its nutrition is derived from the photosynthetic products of the alga. The algal requirement for light limits the depth to which reef-building corals can live and form new reef matrix.

Because coral reef communities are among the most diverse assemblages in the marine environment, and because coraline skeletal material provides the physical substrate for the reef, it goes without saying that the loss of the coral makes the balance of the reef community vulnerable. Although coral reefs occupy less than 0.25% of the marine environment, this community contains more than 25% of marine fishes, and in terms of total species diversity coral reefs are the marine analogue of tropical rainforests. There are three aspects of future climate scenarios that raise concerns regarding the viability of some coral reefs. These factors include rising sea level, elevated seawater temperature, and increased concentrations of dissolved inorganic carbon. Their combined and possibly synergistic effects could in the next few decades put coral reefs at greater risk than at any time in the Quaternary. How can this be so if the onset of the Holocene was characterized by these same three changes in the environment of the coral? Extant coral species apparently survived the climate oscillations of multiple ice age cycles during the last million years, so why should they be considered vulnerable to changes in climate that are likely to occur in the near future?

Sealevel has risen 1 to 2 mm yr^{-1} in the twentieth century, and with projected melting of glaciers and thermal expansion it could rise as much as 2 to 9 mm yr^{-1} during the twenty-first century (Warrick et al., 1996). Given that the rate of sea-level rise early in the Holocene was much greater than this, and coral reefs survived, there is little reason to expect that sea-level rise associated with future climate change will be detrimental to coral reefs. The effect may, however, be different for reefs that have been damaged by coastal development pressures (Zann, 1994).

Changes in ocean chemistry resulting from higher CO_2 levels are likely to be more serious threats to the health of coral reef communities. Aragonite saturation in seawater is today about 390%. This will decline with increasing CO_2 concentration and the corresponding reduction in pH. Calculations suggest that aragonite saturation will decline by approximately 30% at atmospheric CO_2 concentrations twice the preindustrial level. Until recently it had been thought that as long as a high degree of saturation was sustained, the effect on biogenic calcification rates would be negligible. Initially, curious results in the Biosphere II study reported by Chris Langdon and colleagues at scientific meetings (Pennisi, 1998; Kleypas et al., 1999) and laboratory studies conducted by Gattuso et al. (1998, 1999) suggested that serious reductions in calcification rates occur when aragonite saturation declines, even though it remains supersaturated. Using 1992 IPCC scenarios, Gattuso et al. (1999) calculate that a doubling of preindustrial CO_2 will result in a 9 to 30% reduction in coral calcification rates. A similar exercise using the Hamburg ocean carbon model with increasing atmospheric CO_2, and assuming that ocean circulation remains just as it is today, suggests that aragonite precipitation in the tropics has already decreased by 6 to 11% and will decline another 8 to 11% when CO_2 concentrations become twice their preindustrial level (Kleypas et al., 1999). It is also possible that reduced rates of calcification will make reef corals more susceptible to storm damage (Done, 1999).

A final threat to coral reefs is a condition known as bleaching, which occurs when the corals lose their symbiotic algae in response to environmental stress. Some corals do recover following brief periods of bleaching, although the means by which the algae become reestablished is highly speculative. If this fails to happen, the coral tissue dies, leaving the calcareous reef substratum exposed to physical damage and dissolution. Experiments have shown that this condition can be caused by elevated temperatures, reduced salinity, and excessive suspended fine particulate matter, and one or more of these factors have been associated with numerous observed bleaching events (Glynn, 1984; Goreau, 1992; Berkelmans and Oliver, 1999; see also Chapter 12). There is also evidence that at elevated temperatures virulence of bacterial pathogens of corals may increase and that these may be involved in the bleaching process (Kushmaro et al., 1996, 1998).

Corals in today's tropical and subtropical oceans are very near their upper limits for temperature (some within 2°C) during the warm seasons of the year (Goreau, 1992). Although it is not unusual for organisms to have skewed thermal response curves, with steeper gradients at the upper end of thermal tolerance, coral may exhibit more of a threshold response in its loss of zooxanthallae at a critical temperature. This reaction is probably sensitive to both the magnitude of the increment of temperature and the rate at which this increase is experienced. Bleaching that isn't necessarily fatal can occur in response to an increase as small as 1°C above normal seasonal maxima (Brown et al., 1996). There is evidence that thermal anomalies > 3°C are fatal to several coral species (Brown and Suharsono, 1990). With the death of coral tissue the reef substrate is subject to erosion from physical and dissolution processes and colonization by other organisms, especially seaweeds.

In the last two decades the reports of coral bleaching have increased, and several of these were coincident with warm periods of the ENSO cycle. For example, Glynn (1984) documented a massive bleaching event in the Pacific off Panama during the 1982–1983 El Niño. The Great Barrier Reef has also experienced several widespread bleaching events over this period, the most severe of which occurred in 1998 (Berkelmans and Oliver, 1999). What apparently isn't known from laboratory experimentation is whether projected temperature changes for the twenty-first century could be tolerated by corals if they occurred more slowly than in the instance of recent El Niño events.

In this context, the climate data from the LPTM have a clear and startlingly optimistic lesson. The abrupt climate warming due to the injection of methane (and consequently, CO_2) into the atmosphere at the LPTM reduced the aragonite saturation state of the surface ocean in the same manner as is occurring today. The temperature shock from the pulse of greenhouse gases must have been equally severe. Indeed, a large carbonate dissolution event is observed in deep-sea sediments, associated with the carbon isotope excursion (Zachos et al., 1993), suggesting that the oceans did experience a carbonate saturation crisis. However, there is no evidence for the turnover or mass extinction of any marine organisms other than benthic foraminifera. This does not mean that coral reefs will not be affected in a noticeable way, as we have already seen a dramatic decline in the health of coral reef ecosystems on a global scale. But even if the health of reefs diminishes with an enormous decline in spatial extent, the records from the Eocene suggest that the biodiversity of corals will not be affected in a dramatic fashion. Of course, it is possible that additional impacts of human activities, including pollution and land-use changes, in combination with stress from climate change, might exceed whatever tolerance these ecosystems have for adapting to rapid changes. Understanding the physical–chemical–biological coupling in such instances of multiple stresses may be at present a Herculean task for modern oceanography. But with continued progress in observations and modeling, both in the modern and the geologic past, this may be one of the most exciting challenges and most fruitful directions for future oceanographic research.

8. Summary

The effects of rising levels of atmospheric carbon dioxide due to human activities represent a challenge to the study of biological–physical interactions in the ocean. Although some progress has been made in observing such interactions over short time scales, measuring the response of ecosystems to physical variability in the ocean is plagued with uncertainty over how environmental conditions may be changing with time. Climate change scenarios can be developed using coupled atmosphere–ocean models to make some predictions of the response of the ocean to anthropogenic climate change over the next century. But these models have large uncertainties and generally lack the ability to simulate the full range of physical–chemical–biological coupling necessary to understand and predict the possible responses to human actions. In the face of these challenges, there exists information about Earth system response to high levels of CO_2 from reconstructions of the geologic past when similar conditions existed. The Eocene epoch was the most recent time in Earth history when CO_2 levels were comparable to what is predicted for the next century. The inability of climate models to simulate the Eocene climate properly reminds us that these models, tuned to modern conditions, may be inadequate for simulating high levels of CO_2 not seen for 40 million years or more. At the beginning of the Eocene epoch, the abrupt release of methane from deep-sea sediments during the LPTM represents the closest approximation in Earth history to anthropogenic emissions of CO_2. The extinction of many groups of benthic foraminifera gives credence to concerns that future warming may affect deep-ocean circulation and biological interactions on the seafloor. The lack of any major extinctions other than benthic organisms may be good news for the biological scenarios for global warming. Additional lessons may be gained from more careful examination of the Eocene and the LPTM. In particular, a detailed analysis of the biological response to the event across a variety of ecosystems has not yet been completed. In addition, the turnover of benthic foraminifera as well as the lack of major extinctions in other groups raises intriguing questions about the biological response to climate perturbations. Future research aimed at a more detailed understanding of the relationship between biological processes and ocean stratification and mixing through a perturbation such as the LPTM may provide additional lessons for understanding how the ocean will behave through the next century. Incorporating these lessons into our simulations of the biological–physical interactions in the modern ocean is a challenge for the next decade of research.

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