Reports

Phytoplankton Bloom Produced by a Receding Ice Edge in the Ross Sea: Spatial Coherence with the Density Field

Abstract. *Measurements of chlorophyll, particulate carbon, and biogenic silica concentrations near a receding ice edge off the coast of Victoria Land, Antarctica, indicated the presence of a dense phytoplankton bloom. The bloom extended 250 kilometers from the ice edge and was restricted to waters where the melting of ice had resulted in reduced salinity. The region involved was one of enhanced vertical stability, which may have favored phytoplankton growth, accumulation, or both. Epontic algae released from melting ice may have served as an inoculum for the bloom. Ratios of organic carbon to chlorophyll and biogenic silica to carbon were unusually high, resulting in high biogenic silica concentrations despite only moderately high chlorophyll levels.*

Recent studies have shown the importance of the marginal ice zone in polar regions, both with regard to air-ocean energy exchange (*1*) and food web dynamics (*2*). Because of the large area that experiences seasonal ice advance and retreat in the Southern Ocean (*3*), the influence of the ice-edge zone in the Antarctic would be expected to be pronounced. One potentially significant impact of ice-edge regions is their influence on phytoplankton distributions. Marginal ice zones support large blooms of phytoplankton (*4*), although the spatial and temporal extent as well as the causal mechanisms of the blooms are poorly understood. If such blooms are a regular feature of ice-edge regions and the Southern Ocean, they may provide an important food source for the large populations of herbivores, principally krill (*Euphausia superba*), that are found in Antarctic waters.

Several mechanisms have been hypothesized to explain the formation of ice-edge blooms. The primary hypothesis suggests that meltwater from a receding ice pack imparts a degree of vertical stability to an otherwise homogeneous water column (*5*). Under stratified conditions, photosynthetic production should proceed in accordance with the critical depth concept (*6*). A second phenomenon that may affect phytoplankton in marginal ice zones is ice-edge upwelling. Numerical models of ice-edge upwelling (*7*) clearly show its potential importance, and upwelling has been observed in two separate ice-edge studies in the Arctic (*8*). However, because surface nutrient concentrations in the Antarctic are extremely high (*9*), it is unlikely that increased flux of nutrients into the surface layer would result in increased growth of phytoplankton. The importance of upwelling to arctic systems, where surface nutrient levels are often low (*4, 10*), may be greater than in the Southern Ocean. A third hypothesis to account for ice-edge blooms is the accumulation in the euphotic zone of epontic algae (those associated with the pack ice) that had been released into the water column from the melting ice. Ice algae reach high standing stocks (*11*), and their release into the water column represents a potentially large input of biogenic material to the pelagic domain. A refinement of this hypothesis is that, although not all species in the epontic community may remain in the water column as members of the phytoplankton, certain species may act as an inoculum for an ice-edge bloom and actively grow in a vertically stable water column. If algal input from melting ice were important, it would be expected that the taxonomic composition of the epontic and ice-edge phytoplankton communities would be similar. However, presently available data do not allow such a generalization to be made (*11, 12*). It is important to note that these hypotheses are not mutually exclusive and that the importance of each may vary with location, time, and environmental conditions.

In January and February 1983 we conducted measurements aboard the U.S. Coast Guard cutter *Glacier* to determine the extent of the region influenced hydrographically by the receding ice edge and to investigate the magnitude and extent of any ice-edge phytoplankton bloom. Hydrographic stations were occupied in sections normal to the ice edge, which generally followed the coastal contour. Station locations in one of these sections are shown in Fig. 1. Station spacing was based on ice coverage and the results of earlier sections (*13*). Each station consisted of a CTD cast (*14*) and a hydrographic cast in which water from nine depths (maximum, 150 m) was collected. Subsamples for measurement of chlorophyll, particulate carbon, biogenic silica, and other biological variables were taken and either processed at sea or filtered for later laboratory analysis (*15*).

Ice conditions in the study area were variable. Heavy ice cover (virtually 100 percent) was encountered near the coast (station 36), and station 37 was at a distinct boundary between heavy ice and broken ice. Ice cover in the middle portion of the section (stations 38 and 39) ranged from 20 to 60 percent, whereas stations 40 through 43 were in open water. The entire transect was sampled within a 32-hour period. Although the marginal ice zone can respond rapidly (within hours or days) to physical forcing (*8*), meteorological conditions were rela-

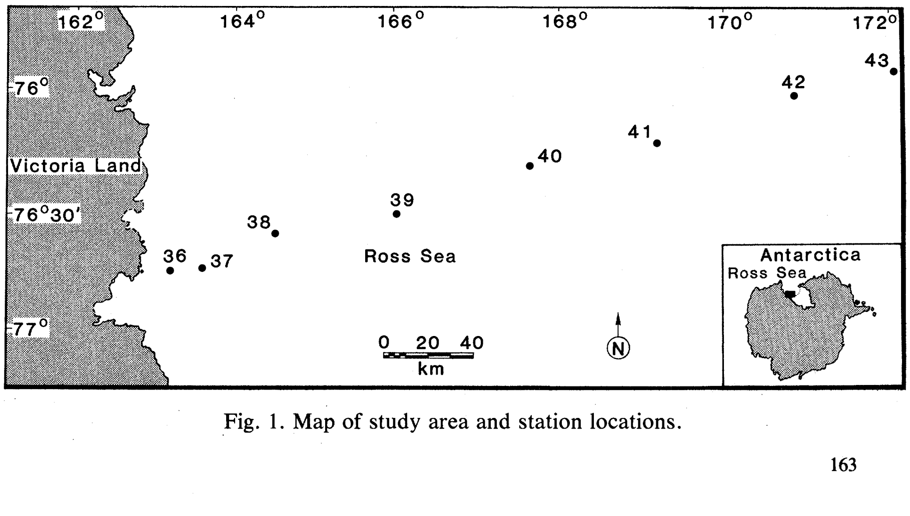


Fig. 1. Map of study area and station locations.

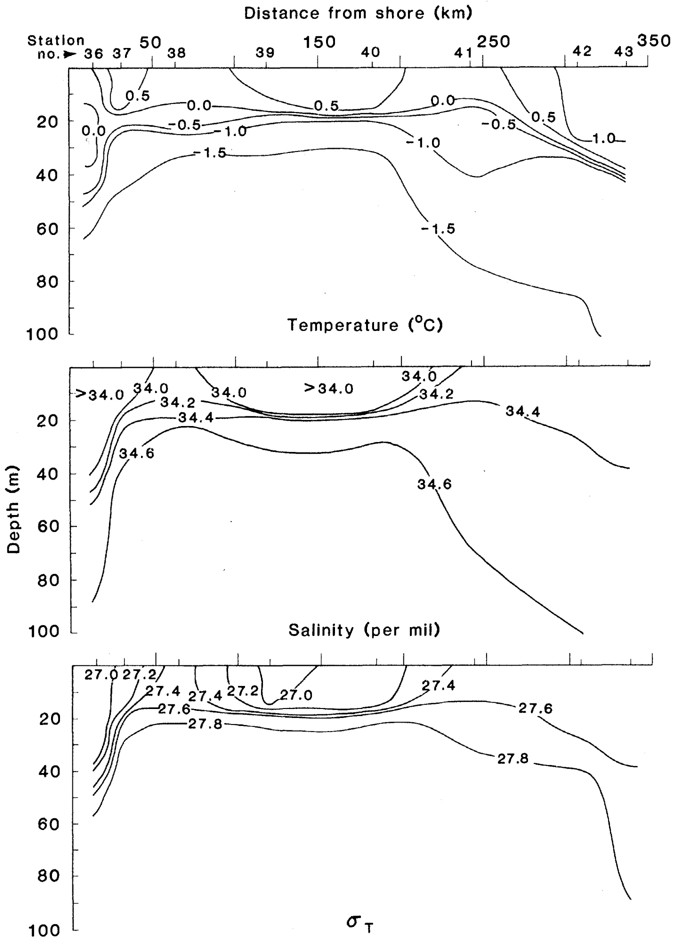
Table 1. Surface and integrated (from 0 to 150 m) measures of biomass at the stations along the transects. Total depth of station 36 was only 95 m.

Measure	Station							
	36	37	38	39	40	41	42	43
Surface chlorophyll (μg/liter)	4.5	3.6	1.7	3.4	4.7	1.2	1.0	0.7
Surface particulate carbon (μmol/liter)	18.6	37.5	31.0	49.0	61.4	39.6	15.9	7.7
Surface biogenic silica (μmol/liter)	13.5	21.3	16.9	30.2	42.1	22.6	10.7	4.3
Integrated chlorophyll (mg/m^2)		146	224	322	204	232	107	63
Integrated particulate carbon (mmol/m^2)		2073	2429	3515	2561	2242	2415	1497
Integrated biogenic silica (mmol/m^2)		950	1134	1577	1140	1073	505	295

tively constant and probably did not produce marked changes in the measured variables during our sampling of the section.

Sections of temperature, salinity, and density (*9*) clearly showed the influence of the melting pack ice (Fig. 2). A layer of low-salinity water was present at the surface and extended about 200 km from dense pack ice at station 37. Lowest salinities and densities were recorded under the heaviest ice cover, indicating active melting. The low-salinity lens extended about 250 km offshore, producing a sharp halocline and pycnocline at a depth of 20 to 30 m. Farther offshore from this feature, surface salinity and the depth of the mixed layer increased markedly.

Phytoplankton biomass, as measured by chlorophyll, particulate carbon, and biogenic silica distributions, was tightly coupled to the region of melt water influence (Fig. 3). The phytoplankton bloom was, in fact, embedded in the meltwater lens. Dominant species in the bloom were the pennate diatom *Nitzschia curta*, which constituted up to 85 percent of the total cell number, and the congeneric species *N. closterium* (*16*). The strong spatial coherence between the zone of lowered salinity and the standing stock of phytoplankton is evidence that phytoplankton abundance and vertical stratification are causally related, but the relation appears to be different from the classical vertical stability mechanism (*6*). The amount of phytoplankton material per unit volume was substantially greater in the bloom (stations 36 to 41) than seaward of it (stations 42 and 43), but the major compositional ratios and relative species abundances of the surface phytoplankton did not change appreciably (Table 1). It thus appears that, offshore of the meltwater lens, the bloom was dissipated by both vertical and lateral processes and that the phytoplankton at the



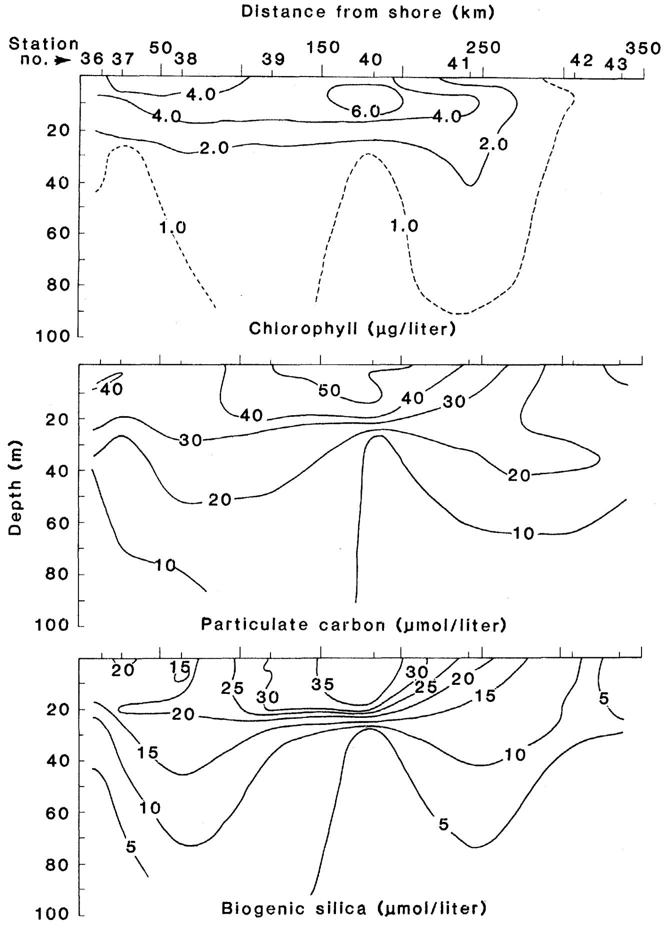


Fig. 2 (left). Vertical section of temperature, salinity, and σ_T along the transect. Sigma-T is the density of seawater expressed as $1000(\rho_T - 1)$, where ρ_T is the density at temperature T of seawater at 1.0 atm in grams per cubic centimeter. Fig. 3 (right). Vertical section of chlorophyll, particulate carbon, and biogenic silica along the transect.

eastern end of the transect were influenced strongly in their composition by remnants of the bloom. Furthermore, the decrease in stratification away from the meltwater input allowed for more active mixing in the water column, resulting in a net transport of phytoplankton to greater depths and spatial limitation of the bloom's surface manifestation.

While the meltwater created a stable environment for phytoplankton accumulation, it also appears that the epontic algae may have served an important role as a bloom inoculum. *Nitzschia curta* is usually found as a member of the epontic community (*17*) and was present in an ice sample taken near our study area. Microautoradiographic analysis showed that *N. curta* was actively photosynthesizing in the bloom (*16*). We do not have enough data on the occurrence and viability of *N. curta* cells in the ice in this study area to say with certainty that the ice provided a seed population of *N. curta* for the bloom. However, the indirect evidence points to the likelihood of such a process.

The similarity between stations in the bloom and those seaward of it with respect to major elemental and species composition of the phytoplankton, along with the fact that the major phytoplankton species both within and seaward of the bloom is a pennate diatom of presumed epontic origin, suggest the following sequence of events at a receding ice front:

1) Meltwater and epontic algae are introduced into the surface layer in areas of active melting.

2) Certain species of epontic algae are capable of growth in the meltwater lens (in this case the most obvious of these species were *N. curta* and *N. closterium*).

3) A stable layer of meltwater retards vertical mixing and thus allows the algal species that are growing most rapidly to accumulate and form a local biomass maximum.

4) The meltwater lens is continuously being degraded at its seaward edge by vertical mixing. This results in the phytoplankton at locations seaward of the meltwater lens having the same elemental and species composition as within it, but at lower absolute concentrations and mixed over a greater vertical extent. These cells may or may not continue to grow in the more deeply mixed water column.

The absolute levels of chlorophyll encountered in the bloom were higher than those observed in most previous studies in the Southern Ocean, but typical of values normally encountered in productive coastal regions (*9*). Particulate carbon values, however, were extremely high, resembling the concentrations found in hyperproductive upwelling areas, such as those off the coast of Peru (*18*). Concentrations of biogenic silica in this bloom were, to our knowledge, the highest ever reported in the ocean. They averaged approximately three times higher than the concentrations off the coast of northwest Africa (*19*), which had the highest previously known levels. Measurement of only a single parameter, such as chlorophyll, would have led to erroneous conclusions about the bloom's magnitude because of its anomalous composition.

The difference between the composition of phytoplankton in this bloom and that elsewhere in the ocean can be appreciated by examining carbon/chlorophyll and silica/carbon ratios. The mean carbon/chlorophyll ratio for the euphotic zone was 118.2. Data on various natural populations indicate that, for populations not limited by nutrients, a ratio of 25 to 40 is expected; higher ratios are produced during nutrient limitation (*20*). However, it has also been shown that low temperatures can result in elevated carbon/chlorophyll ratios (*21*), and in other field studies in Antarctic waters elevated ratios have been measured, although they are not uniform throughout the Southern Ocean (*4, 9*). The mean mole ratio of biogenic silica to organic carbon in our euphotic zone samples was 0.62; oceanic phytoplankton generally exhibit a ratio of about 0.13 (*22*). Over 90 percent of the diatom frustules in samples from this bloom were associated with physically intact cells with readily detectable chloroplasts, and microautoradiography detected activity in most cells (*16*); thus the elemental ratios reported here do not appear to be affected significantly by detrital biogenic material. Recent studies of elemental uptake of dissolved nitrate, phosphate, and silicic acid (*24*) indicate that biogenic silica/carbon ratios in the Antarctic can be quite different from those in other oceanic regions. It is also noteworthy that polar diatoms appear to be highly silicified when viewed microscopically. Up to 85 percent of the phytoplankton cells in this bloom were of the species *Nitzschia curta* (*16*); the high carbon/chlorophyll and silica/carbon ratios we observed almost certainly imply an anomalous composition of this species. However, a composition similar to that which we observed may be a much more general phenomenon (*4, 9, 23*). While elevated carbon/chlorophyll ratios may reflect temperature effects on cellular processes, high silica/carbon ratios may represent an evolutionary modification of the elemental composition of Antarctic diatoms resulting from growth in a continuously nutrient-replete environment.

Ice-edge blooms may constitute a large pulse of biogenic material that remains in the water column for only short periods. Therefore the yearly contributions of photosynthetically fixed carbon to the pelagic realm of the Southern Ocean may have been underestimated in previous studies (*24*). Nutrient depletion calculations suggest strongly that this is the case in the Weddell Sea (*25*). The fate of this material produced in ice-edge blooms remains uncertain. Higher trophic levels may have life strategies keyed to exploiting this resource (*26*), and this organic input may help to support the large invertebrate, fish, and mammal populations of the Southern Ocean. Conversely, much of the material may not be utilized at the surface but transported to the sea floor. The biomass of benthic organisms on the Antarctic continental shelf is large (*27*) and must derive its energy from phytoplankton production. It is noteworthy that the Southern Ocean has massive deposits of diatomaceous oozes estimated to constitute 80 percent of the world's recent deposition (*28*). The western Ross Sea has recently been reported to be an area where siliceous sediments are accumulating rapidly (*28*), and the diatom assemblage in those sediments contains a high proportion of *N. curta* frustules (*17*). Such findings, when combined with our own, suggest that ice-edge blooms of phytoplankton may constitute a quantitatively important source of these deposits.

WALKER O. SMITH
Botany Department and *Graduate Program in Ecology, University of Tennessee, Knoxville 37996*
DAVID M. NELSON
College of Oceanography,
Oregon State University,
Corvallis 97331

References and Notes

1. N. Untersteiner, *Air-Sea-Ice: Research Programs for the 1980's* (University of Washington, Seattle, 1983); G. Kukla and J. Gavin, *Science* **214**, 497 (1981).
2. V. Alexander, *Cold Reg. Sci. Technol.* **2**, 157 (1980); M. Bradstreet and W. E. Cross, *Arctic* **35**, 1 (1982).
3. The area of seasonal ice cover in the Southern Ocean has been estimated to be 14×10^6 to 18×10^6 km^2 [H. Zwalley *et al.*, *NASA Weather Clim. Rev. Pap. 56* (1979)], although significant annual variations occur.
4. V. Alexander and J. Niebauer, *Limnol. Oceanogr.* **26**, 1111 (1981); C. P. McRoy and J. J. Goering, in *Oceanography of the Bering Sea*, D. W. Hood and E. J. Kelley, Eds. (University of Alaska, Fairbanks, 1974), pp. 403–421; S. Z. El-Sayed, in *Biology of the Antarctic Seas*, G. Llano and I. Wallen, Eds. (American Geophysical Union, Washington, D.C., 1971), pp. 301–312; S. Z. El-Sayed and S. Taguchi, *Deep-Sea Res.* **28A**, 1017 (1981).

5. P. T. Marshall, *J. Cons. Int. Explor. Mer.* **23**, 173 (1957).
6. H. U. Sverdrup, *ibid.* **18**, 287 (1953).
7. A. J. Clarke, *Deep-Sea Res.* **25**, 41 (1979): L. P. Røed and J. J. O'Brien, *J. Geophys. Res.* **88**, 2863 (1983).
8. J. R. Buckley, T. Gammelsrod, J. A. Johannessen, O. M. Johannessen, L. P. Røed, *Science* **203**, 165 (1979); O. M. Johannessen, J. A. Johannessen, J. Morison, B. A. Farrelly, E. A. S. Svendsen, *J. Geophys. Res.* **88**, 2755 (1983).
9. For example, surface nitrate concentrations in waters south of the Antarctic convergence rarely fall below 10 μM [S. Z. El-Sayed, in *Antarctic Ecology*, M. W. Holdgate, Ed. (Academic Press, New York, 1970)]. In our study the mean surface nitrate concentration was 10.2 μM (D. Nelson *et al.*, in preparation).
10. S. L. Smith, W. O. Smith, L. A. Codispoti, paper presented at the American Geophysical Union/American Society of Limnology and Oceanography Ocean Science Meeting, New Orleans, February 1984.
11. A. C. Palmisano and C. W. Sullivan, *Polar Biol.* **2**, 171 (1983); S. F. Ackley, K. R. Buck, S. Taguchi, *Deep-Sea Res.* **26A**, 269 (1979); R. A. Horner, *Oceanogr. Mar. Biol.* **14**, 167 (1976).
12. L. Schandelmeier and V. Alexander, *Limnol. Oceanogr.* **26**, 935 (1981); T. J. Hart, *Discovery Rep.* **21**, 263 (1942).
13. Three sections were sampled, with stations 36 through 43 being the middle transect. The same section was surveyed 5 days earlier [W. O. Smith and D. M. Nelson, in *Fourth Symposium on Antarctic Biology*, L. W. Siegfried, Ed. (Elsevier, Amsterdam, in press)].
14. A CTD is an instrument that continuously records conductivity, temperature, and pressure as it is lowered through the water. From these measurements salinity and density can be calculated.
15. Chlorophyll was analyzed fluorometrically on samples filtered through Gelman A/E glass fiber filters and extracted in 90 percent acetone. Particulate carbon was collected by filtration of seawater through precombusted Gelman A/E glass fiber filters, dried at 60°C, and analyzed on a Perkin-Elmer model 240B elemental analyzer. Biogenic silica, a measure of the silicon incorporated into diatom and silicoflagellate tests, was determined by filtering seawater through 0.4-μm Nuclepore filters, drying the filters at 60°C, digesting the filters in hot sodium hydroxide, and determining the resulting concentration of silicic acid by colorimetry.
16. D. L. Wilson, W. O. Smith, D. M. Nelson, paper presented at the American Geophysical Union/American Society of Limnology and Oceanography Ocean Science Meeting, New Orleans, February 1984.
17. R. S. Truesdale and T. B. Kellogg, *Mar. Micropaleon.* **4**, 13 (1979).
18. L. A. Hobson, D. W. Menzel, R. T. Barber, *Mar. Biol.* **19**, 298 (1973).
19. W. M. Krebs, *Micropaleontology* **29**, 267 (1983).
20. T. R. Parsons, M. Takahashi, B. Hargrave, *Biological Oceanographic Processes* (Pergamon, New York, 1977), pp. 50–60.
21. W. K. W. Li, in *Primary Productivity in the Sea*, P. Falkowski, Ed. (Plenum, New York, 1980), pp. 259–279.
22. D. M. Nelson and L. I. Gordon, *Geochim. Cosmochim. Acta* **46**, 491 (1982).
23. S. leJehan and P. Treuger, in *Fourth Symposium on Antarctic Biology*, L. W. Siegfried, Ed. (Elsevier, Amsterdam, in press).
24. O. Holm-Hansen *et al.*, in *Adaptations within Antarctic Ecosystems*, G. Llano, Ed. (Gulf, Houston, 1977), pp. 11–50.
25. J. C. Jennings, L. I. Gordon, D. M. Nelson, *Nature (London)* **308**, 51 (1984).
26. G. E. R. Deacon, *Deep-Sea Res.* **29**, 1 (1982); J. Tranter, *Oceanogr. Mar. Biol.* **20**, 11 (1982).
27. I. Everson, *The Living Resources of the Southern Ocean* (Food and Agricultural Organization, Rome, 1977), pp. 27–33.
28. D. DeMaster, *Geochim. Cosmochim. Acta* **45**, 1715 (1981); S. E. Calvert, in *Silicon Geochemistry and Biogeochemistry*, S. R. Aston, Ed. (Academic Press, New York, 1983), pp. 143–186; D. DeMaster and P. Hoffman, in preparation.
29. Supported by NSF grant DPP81-19572 and by the Office of Naval Research while one of us (W.O.S.) occupied the Arctic Chair in Marine Science at the Naval Postgraduate School, Monterey, Calif. J. Ahern, M. Carbonell, J. Elser, S. Moore, C. Weimer, P. Whaling, and D. Wilson assisted in the study. Order of authorship was determined by coin toss.

13 June 1984; accepted 11 October 1984

Sea-Floor Hydrothermal Activity Links Climate to Tectonics: The Eocene Carbon Dioxide Greenhouse

Abstract. *Two important findings of recent ocean-floor drilling in the southeast Pacific (Deep Sea Drilling Project Leg 92) are (i) that sea-floor hydrothermal activity may fluctuate through time by as much as an order of magnitude and (ii) that episodes of greatest hydrothermal flux correspond to times when ridge-transform plate boundaries are undergoing major changes in their configuration rather than to known times of increased spreading rate or volcanism. Evidence is presented here in support of the hypothesis that heightened hydrothermal activity induced by the Eocene tectonic activity caused a global greenhouse effect, which may represent the long-sought-after historical analog to the carbon dioxide–induced global warming expected to occur by the middle of the next century.*

The idea that changes in atmospheric CO_2 concentrations can affect global surface temperatures was first postulated nearly a century ago (*1–3*). This connection not only is now well documented and widely accepted but also has aroused much concern. Increased CO_2 inputs during the next several decades, primarily from the cumulative effects of deforestation and fossil-fuel combustion, are expected to double the atmospheric CO_2 load thought to have been present in 1900 (*4*). Various numerical models predict that this CO_2 doubling will lead to a greenhouse effect, manifested as an increase of about 1.5° to 4.5°C in the mean global surface temperature by the middle of the next century (*5*).

This anthropogenically induced change in atmospheric composition has been viewed as both a massive and an unprecedented geophysical experiment (*5, 6*). That it is occurring now on a large scale is clear; it is far less certain, however, that it has not occurred before. Indeed, there is abundant paleontological, paleoceanographic, and paleogeographic evidence in support of the idea that relatively warmer periods occurred during the past (*7–9*). Revelle (*3*) has suggested that paleoclimatic reconstructions of these periods could be used to evaluate and verify the predictions of mathematical models (which contain certain troublesome uncertainties) and could provide useful clues to the consequences of future warming trends. Unfortunately, the application of this earth-model approach to past time periods is hampered by a limited data base and inherent chronological errors, whereas investigations of more recent periods must grapple with uncertainties concerning the role of CO_2 in global warming events. For example, both the warm climate of the early Holocene and glacial-interglacial temperature oscillations have been related to changes in the earth's orbit. These changes in atmospheric CO_2 concentrations may have been responses to rather than causes of the associated climate changes (*5*). For this reason, one conclusion of a recent review of studies concerning the anticipated CO_2 greenhouse effect was that there is no satisfactory historical analog (*5*). We suggest here that CO_2-induced climate changes have occurred, that they were caused by pulsations in the intensity of sea-floor hydrothermal activity induced by tectonic rearrangements of sea-floor spreading centers, and that the most obvious example of this process occurred in the early Eocene.

This suggestion of an inferred link between ocean tectonics and atmospheric CO_2 concentrations is based upon correlations between certain parameters of tectonism (for example, spreading rates) and sea level changes, the occurrence of oolites in the stratigraphic record of the Phanerozoic, and computer-simulated variations in the carbonate-silicate geochemical cycle over the past 100 million years (m.y.) (*10–13*). A direct chemical link between sea-floor processes and CO_2 fluxes was revealed recently by the discovery of widespread hydrothermal activity along oceanic ridges. Fissures and fractures formed in fresh ridge-crest basalt as it cools and is rifted apart provide conduits for the circulation of cold bottom waters into the underlying crust. The circulating seawater penetrates to depths of a few kilometers, reacts chemically with hot basalt at temperatures in excess of 300°C, and emerges as hot springs along the ocean floor (*14*). The chemical exchanges that occur during this process include the removal of magnesium and sulfate from seawater and concomitant enrichment of calcium, potassium, silica, iron, manganese, and other trace elements within the hydrothermal solution (*14–18*).

The chemical exchange of calcium for magnesium in this process is particularly